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PROTOPLASMIC SYSTEMS AND GENETIC CONTINUITY¹

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THE cell is a complex heterogeneous system that arises only by division of a preexisting system of the same general type, and with certain minor qualifications the same is true of each of its two primary components, nucleus and cytosome—each of these is itself a complex system that arises by division of a preexisting system. Cells may thus reproduce themselves for a period that has no assignable limits. We long since learned, accordingly, to think of cell-division as the central phenomenon in heredity, yet prolonged research has left us uncertain concerning many of its problems.

So far as nuclear division (karyokinesis) is concerned our analysis is now well advanced. The progress of investigation, both cytological and genetical, long since demonstrated that karyokinesis is a meristic process involving a spinning out of the nuclear substance into long threads (spireme) and their longitudinal fission, by which is accomplished a precise doubling and equal distribution of all the essential components of the system (chromosomes, chromomeres, genes, etc.). Our acquaintance with division of the cytoplasmic system (cytokine-

¹ In substance a lecture given at the Marine Biological Laboratory, Woods Hole, July 10, 1925.

sis) is, on the other hand, in a very backward state. Superficially regarded, the process offers the general aspect of a simple mass-division; and as such it has rather generally been regarded. Cytokinesis shows in fact nothing exactly comparable to the spinning out of the nuclear substance to form dividing spireme-threads and chromosomes. Nevertheless, the researches of recent years have prominently raised the question whether cytokinesis should not, like karyokinesis, be regarded as meristic in type, even though it be less exact in operation.

It has been rather generally held, probably correctly, that many formed components of the cytosome (granules, fibrillae, etc.) arise epigenetically ("*de novo*") in the hyaloplasm without discoverable direct connection with their predecessors in earlier generations; though the possibility has always remained that some of them might grow from preexisting smaller bodies lying below the horizon of microscopical vision.² I will not discuss this possibility here nor enter into speculations concerning a supposed ultra-microscopical metastructure of protoplasm (micromerism, pangenesism, etc.). For the present we are more interested in questions raised by direct observations on the visible formed cytoplasmic components, in particular the central bodies, plastids, chondriosomes and Golgi-bodies. Both plastids and centrioles, admittedly, are capable of self-perpetuation by growth and division, though it is not certain that plastids have no other mode of origin, and it now seems to have been finally demonstrated that under certain conditions centrioles may arise *de novo*. In respect to the chondriosomes and Golgi-bodies the status of the question is much more doubtful, though it is known that both may at times break up into smaller bodies by some sort of division or fragmentation. Both these kinds of bodies are of especial interest, for many reasons, in connection with the problem of genetic continuity in cell-systems. With the advance of research the probability grows that chondrio-

² Altmann, Heidenhain. See Wilson, 1923, 1925.

somes are omnipresent in the cells of both animals and plants; and, in the case of animals at least, the same may be said of the Golgi-bodies. It is certain that each of these kinds of bodies consists of a specific material capable of great if not unlimited growth. It has been made clear that in a large class of cases both are received as such from the mother-cell during mitosis (chondriokinesis, dietyokinesis). What does not yet clearly appear is whether either or both are self-propagating in the same sense as chromosomes, plastids or centrioles.

In addition to the foregoing facts we may emphasize the presence of chondriosomes and Golgi-bodies in relatively undifferentiated cells having extremely little cytoplasm. For example, in the early germ-cells of scorpions (spermatogonia, spermatocytes) the cytosomes are in certain stages so small that the tissue gives the appearance of a syncytium (though cell-boundaries are in fact present), the cytoplasm being reduced to hardly more than thin films between the large and crowded nuclei; yet both the bodies in question are still conspicuously present (Fig. 1). Here it would almost seem that the cytosome contains little more of the ground-substance or hyaloplasm than suffices to carry forward the chondriosomes and Golgi-bodies (no doubt also the centrioles) to a later period when they play their part in the growth and differentiation of the germ-cells. Such facts indicate that these bodies must be of great importance for the operation and maintenance of the cell-system, even though their physiological rôle has not yet been precisely determined.

There is much in the literature to support the conclusion that both chondriosomes and Golgi-bodies play an important part in the production of other formed components of the cytosome. Recent researches have produced strong evidence that the Golgi-bodies are immediately concerned in the formation of the secretory granules, and the possibility is thus opened that they may be concerned in the production of the organic enzymes

generally.³ There is evidence tending to connect them with the formation of excretory granules and of storage-granules (yolk, fat); and it is certain that they form the source of the acrosome of the animal sperm.⁴ Concerning the rôle of the chondriosomes the case is still widely open. It seems, however, very probable that they are

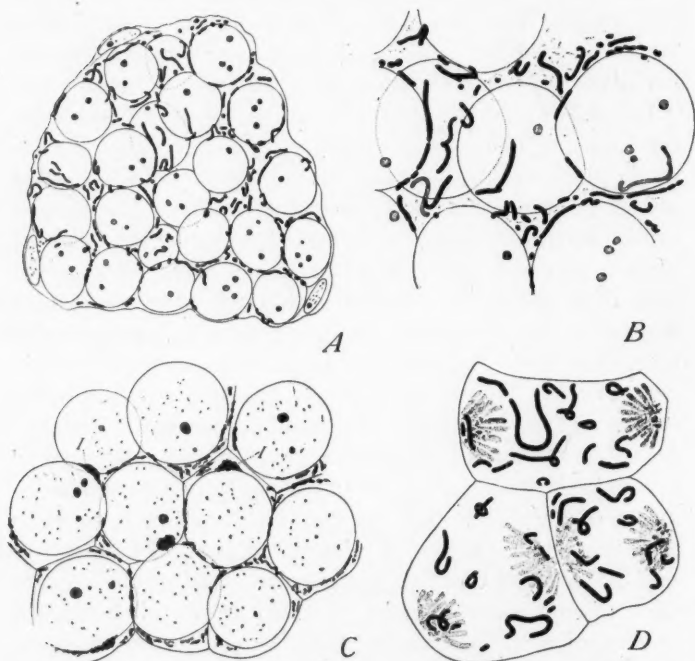


FIG. 1. Spermatogonia (and spermatocytes†) of *Opisthacanthus*
(A $\times 1000+$; B-D $\times 2000+$)

A, section through complete cyst of large spermatogonia (Benda method) with closely crowded nuclei and chondriosomes (black); B, detail from same, more enlarged; C, smaller spermatogonia (perhaps young spermatocytes), Flemming iron-haematoxylin, showing cell-boundaries, chondriosomes (damaged by the fixation) and idiozomes, I (Golgi-apparatus); D, anaphases of mitosis, large spermatogonia (Benda method), sorting out of whole chondriosomes.

³ See Nasonov (1923, 1924), Bowen (1924a).

⁴ See Bowen (1924b), with literature.

centers of specific chemical action (Regaud), perhaps effected by surface-action (Cowdry), a view which fits well with the earlier conclusion of Altmann, Meves, Duesberg, Guilliermond and others that they may be in some manner the source of many other formed bodies, including the various forms of plastids and certain types of granules and fibrillae. This conclusion, it is true, has encountered considerable opposition, and opinion concerning it is still unsettled; nevertheless I believe that it deserves the most careful further consideration. But whatever be the issue of this particular question the known facts sufficiently emphasize the importance of both chondriosomes and Golgi-bodies for every inquiry into the nature and perpetuation of cytoplasmic systems.

The cytological aspects of this subject will here be discussed briefly in the light of studies on the chondriosomes (to some extent also on the Golgi-bodies) of scorpions, on which I have long been engaged. I have examined the history of these bodies in the male germ-line of four genera, namely, *Centrurus* (two species) *Opisthacanthus*, *Vejovis* (two species) and *Hadrurus*. These forms offer material of exceptional interest for the problem because, as heretofore reported (Wilson, 1916), they show two widely different, and at first sight irreconcilable, types of chondriosome-behavior in the spermatocyte-divisions. One of these has thus far been found only in *Centrurus*. Here the chondriosomes, originally small and scattered, enlarge and finally fuse into a single large ring-shaped body which is exactly divided in each spermatocyte-mitosis and the chondriosome-material is thus equally allotted to all the sperms. In the contrasting type, found in the three other genera mentioned,⁵ the chondriosomes remain always separate and enlarge to form much larger rounded chondriospheres of approximately constant number (in *Opisthacanthus*, ± 24). These bodies undergo no division but remain scattered through the cytosome, and

⁵ This type was earlier found by Sokoloff (1913) in *Euscorpius*, more lately by Gatenby and Bhattacharaya (1925) in *Palamnaeus*.

in the course of each spermatocyte-division are sorted out whole into two nearly equal groups (Figs. 2, 3). The second spermatocytes thus receive each about twelve chondriosomes and the spermatids six; but this process is demonstrably inexact.⁶ All theory aside, it is remarkable that bodies so closely similar in their earlier stages, and identical in destiny (formation of the envelopes of the sperm-tail), should differ so radically in mode of distribution to the sperm-forming cells.

In the hope of throwing some light on this puzzle I have attempted to trace the history of the chondriosomes in earlier stages of the germ-line, in so far as they are shown in the mature testis, and incidentally have made some observations on the Golgi-apparatus. In spite of some difficulties this material offers many advantages for such a study. After the earliest stages the chondriosomes are relatively large and few and stain brilliantly by the Benda method and others. The mature gonad contains large numbers of separate cysts of all ages, each composed of numerous cells at nearly the same stage of development. In each cyst the chondriosomes are of the same general type, though cysts of different age differ materially in this respect. Since an enormous multiplication of cells takes place during the growth of the testis, and since numerous chondriosomes are present at every stage, there must be a corresponding multiplication of these bodies. How does this take place?

In respect to this question, so important for our general conceptions of cytoplasmic systems, a conflict of opinion now exists. It is generally, but not unanimously, agreed that the chondriosomes are of strictly cytoplasmic origin. It is certain, as above stated, that in cell-division many of them pass from mother-cell to daughter-cell. Altmann, Benda, Meves, Duesberg, Guilliermond and others have considered them as bodies that are

⁶ Careful counts of 500 spermatids in *Opisthacanthus* showed in round numbers 76 per cent. with six chondriosomes, 17 per cent. with five, and 7 per cent. with seven. In *Vejovis* the variation is somewhat greater.

genetically continuous from generation to generation, a conclusion summed up in Duesberg's statement that "every chondriosome arises from a preexisting chondriosome." (1910, p. 122.) This does not necessarily mean that chondriosomes, like plastids or chromosomes, are definitely organized and self-perpetuating bodies, as originally maintained by Altmann. A cautious attitude in respect to this interpretation was taken by Benda, Meves and Duesberg; but it has been to a certain extent implied in some of the writings of both their followers and their critics. It has been supported by some important researches, prominent among them those of Fauré-Fremiet (1910) on cell-division and chondriokinesis in ciliates, and those which have indicated the identity of plastids (bodies which undoubtedly multiply by growth and division) with chondriosomes or their origin from them. (See Meves, 1917.) A widely different conclusion is reached by Schreiner (1916) whose results demand the most careful attention. This excellent observer found that during the prophases of mitosis in epithelial cells of *Myxine* the long thread-like chondriosomes fragment into much smaller bodies, which are then sorted out whole into the daughter-cells; but he also reached the remarkable conclusion that their numbers are periodically reinforced by new formation from extruded fragments of *nucleoli*. This result, almost alone among those of modern observers, is in principle akin to the earlier ones of Goldschmidt (1904) and his followers, now generally abandoned. A few observers, finally, have concluded that chondriosomes may arise *de novo* in the cytoplasmic substance.

Without attempting here a critical discussion of these divergent views I will briefly summarize the main conclusions concerning them indicated by my studies on the germ-cells of scorpions, as follows:

(1) In the spermatogonia and spermatocytes of these animals not the least evidence has been found that nucleoli or nucleolar fragments are at any stage extruded

from the nuclei, or that chondriosomes have such an origin. All the evidence indicates that at every stage the chondriosomes are strictly cytoplasmic structures.

(2) That chondriosomes may arise *de novo* (i.e., without direct connection with preexisting chondriosomes) has been accepted by a considerable number of observers, both from studies on living material,⁷ and on sections;⁸ and the possibility of such an occurrence is admitted even by Duesberg, a leading advocate of the genetic continuity of chondriosomes (see 1915, p. 62). By neither method, admittedly, is it easy to obtain crucial evidence for or against this possibility; and no conclusions can yet be stated otherwise than tentatively. Nevertheless, the facts observed in cells of the germ-line in scorpions point to the conclusion that in this case, at least, chondriosomes always arise from preexisting ones. Did they form *de novo* we should expect to find among them all gradations in size down to the limit of vision. But in this material such is not the case. In the spermatogonia (Figs. 1, 3, F) they appear in the form of threads and rods, of nearly uniform diameter and with rounded ends, which graduate down to spheroidal mitochondria of nearly this same diameter, or a little less, but do not in general pass much below this limit. Here and there, it is true, still smaller granules of doubtful nature may be seen; but their number seems far too small to form an adequate source of the numerous larger chondriosomes.

(3) On the other hand, in every cyst of spermatogonial anaphases and telophases may be seen the demonstration that the chondriosomes of the mother-cell are being sorted out into two approximately equal groups that pass into the daughter-cells.

(4) The sorting-out process is not accompanied by any general or regular process of division. Especially in certain cysts of larger spermatogonia this is evident beyond the possibility of doubt (Fig. 1, D). The chondrio-

⁷ Chambers (1915), Lewis and Lewis (1915).

⁸ See Schreiner (*ante*), Luna (1913).

somes—here relatively very large, but showing all gradations from long rods through shorter ones down to spheroidal bodies—may with perfect clearness be seen passing to the poles without the least sign of division or fragmentation.

(5) There is nevertheless almost conclusive evidence that the chondriosomes increase in number by a variable process of fragmentation, which in case of the shorter rods often appears as an equal or subequal fission closely similar to that described in the ciliates by Fauré-Fremiet, both *in vivo* and in sections. All stages of this process may be seen, including various degrees of constriction (dumbbells) leading up to separate paired spheroids. In these animals, however, the process is not synchronized with nuclear division. Such figures are seen here and there during mitosis along with many simple rods passing undivided to the poles (Fig. 3 C, D); but they are also of common occurrence in the interphases (Figs. 1, A, B; 3, E). In case of the longer rods and threads the process is much less regular and rarely is seen during mitosis. In the interphases the threads are often single, without sign of fragmentation; but often, too, they show all stages of what I can only interpret as a fragmentation into shorter rods or even spheroidal bodies. The process here seems to be quite irregular; but occasionally the products are seen in regular alignment and in close series (Figs. 1, A, B, D; 3, E). Processes of this type have often been described, both in fixed preparations and *in vivo*;⁹ but their significance has not, I think, been sufficiently recognized. Here again, admittedly, it is difficult to reach a certain conclusion from the study of fixed material alone. Nevertheless, in view of all the facts, it seems highly probable that the longer rods and threads arise by the terminal growth of shorter ones which themselves arise by the fragmentation (in some cases an equal division) of longer ones as above described. In a certain

⁹ See, for instance, Schreiner (1916), Lewis and Lewis (1915), Lewis and Robertson (1916).

sense, therefore, the chondriosomes are self-perpetuating; but this should not be taken to mean that they are autonomous bodies as such. It is, I think, more probable that they are variable, plastic and polymorphic forms assumed by a specific substance which is *per se* capable of extended and perhaps unlimited growth; which arises from a preexisting substance of the same kind, and is genetically continuous in successive generations of cells; but which is not definitely or permanently organized to form individualized structural units.

The distinction thus drawn is, I think, more than a merely verbal one and involves broader questions. To what extent may such a conception apply to other components of the cytoplasmic system? Nearly all recent studies indicate that it may be applicable to the Golgi-bodies, though the facts are here less fully known. The observations of Deineka, Hirschler, Nassonov, Gatenby, Bowen, Cowdry and others have shown that the Golgi-material too is capable of extensive growth; that it is to a considerable extent polymorphic; that at certain stages the Golgi-bodies fragment; that in cell-division the substance of these bodies is passed on in the form of dictyosomes from mother-cell to daughter-cell. With all this my observations on the germ-cells of scorpions are in agreement, though they are admittedly inadequate and must be taken with a certain reserve because based on an unsuitable technique.¹⁰ Nevertheless, the phenomena shown in this material are of such interest as to merit brief mention here. The Golgi-bodies seem to be present at every stage from the spermatids backwards to the earlier generations of spermatogonia, in which the cytoplasm is so scanty as to form only a small fraction of the nuclear volume. During the whole growth-period of

¹⁰ Material fixed especially for the Golgi-bodies (Kopsch method and modifications) failed to give satisfactory results. The following account is based on gonads fixed in strong Flemming's fluid and stained with iron-haematoxylin. In this treatment the Golgi-material has no doubt suffered some damage; but I believe the identification to be correct, and the pictures are in most respects very clear.

the spermatocytes (apparently also in the spermatogonia) the Golgi-apparatus appears in the form of a rounded but somewhat irregular idiozome closely applied to the nucleus, and in later stages is clearly seen to consist peripherally of rodlets or plate-like bodies stained deep black by the haematoxylin and having no connection with the chondriosomes. In the first spermatocyte-division its behavior is of unusual and interesting type. During the middle prophase the idiozome always draws out along the nuclear membrane, and in some cases its main mass is clearly seen dividing into two parts (Fig. 2, B, C), though there are many indications that it may also fragment into a larger number of smaller pieces. I have been unable to follow its later history completely; but in the later prophase what I believe to be the main part of the Golgi-substance is seen approaching the spindle-poles in the form of two fairly definite masses composed of deeply staining rod-like bodies (Fig. 2, D). A varying number of smaller bodies of similar type are however also often seen scattered elsewhere in the cytoplasm. At full metaphase the two masses are always closely applied to the spindle-poles, over which they fit like caps, so that the centrioles, previously clearly visible, are now lost to view (Fig. 2, E, F). In this position the two masses pass into the respective daughter-cells, and during the interphase are seen lying near the nucleus as a plate-like mass (Fig. 3, A). In the second mitosis quite similar masses are again seen at the poles (Fig. 3, B) passing thence into the spermatids, where, as usual, they take part in forming the acrosome. A similar process of dictyokinesis seems to take place in the spermatogonial divisions, though this is less certain owing to the difficulty of distinguishing here between the Golgi-bodies and the chondriosomes (Fig. 3, F).

These observations indicate a mode of dictyokinesis akin to that described by Nasonov (1922) in *Triton* and by Ludford and Gatenby (1921) in mollusks and mammals, but showing an even more definite tendency of the

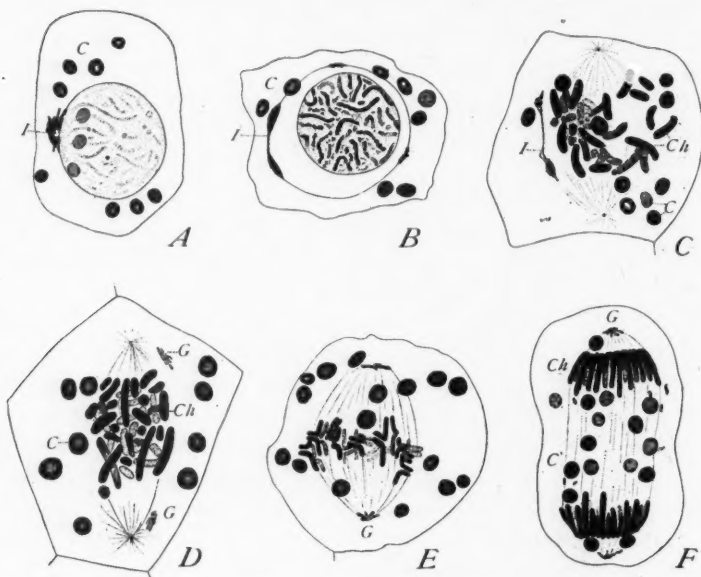


FIG. 2. Primary spermatocytes of *Opisthacanthus* (Flemming-iron-haematoxylin), chondriospheres (C), idiozome and Golgi-apparatus (I, G) and chromosomes (ch. $\times 2000$ +).

A, middle growth-period, with idiozome surrounded by Golgi-bodies, chondriospheres; B, early first-division prophase, contraction-figure, idiozome dividing; C, later prophase, idiozome dividing, centrioles, chondriospheres, chromosomes; D, late prophase, Golgi-masses, passing to the poles; E, first metaphase, Golgi-masses covering the centrioles; F, anaphase of same, showing Golgi-masses at poles and a few scattered Golgi-bodies (?).

dictyosomes to mass at the spindle-poles. These phenomena emphasize the conclusion of Bowen (1920) that chondriokinesis and dictyokinesis involve a relation between the cytoplasmic formed bodies and the division-centers that means more than a merely fortuitous association. Whether the Golgi-material may form in the cytosome *de novo* is an open question on which the attention of cytologists is now closely centered. The possibility of such an origin has been admitted by some of the most recent observers;¹¹ but it seems at least equally pos-

¹¹ See Bramble (1925), Ludford (1925).

sible that the reconstruction of the Golgi-apparatus that follows the breakdown occurring after secretory activity, or in the course of dietyokinesis, may always take its point of departure in preexisting Golgi-material. Aside from this doubtful point both the morphology of this apparatus and its history in cell-division suggest a conclusion analogous to that above outlined in respect to the chondriosomes. The facts indicate that the Golgi-bodies, too, consist of a specific and self-perpetuating stuff that is genetically continuous from one cell-generation to another, but is morphologically polymorphic and not very definitely organized into self-perpetuating structural units. It is an interesting question whether this stuff,

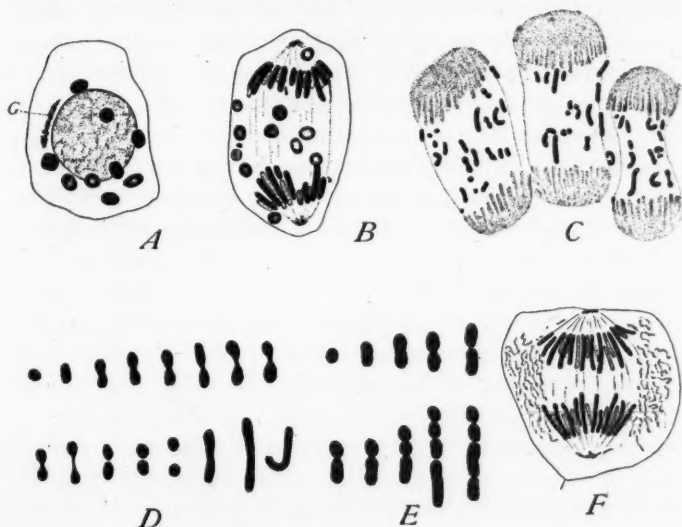


FIG. 3. Various stages of spermatogenesis, *Opisthacanthus* (A, B, C, F, $\times 2000+$, Flemming-haematoxylin, C-E, Benda method). D and E enlarged about twice as much as the other figures.*

A, interkinesis following first division, Golgi-mass at G; B, second division anaphase (Cf. Fig. 2E); C, anaphases of small spermatogonia, a few of the chondriosome-rods constricting; D, various forms of chondriosomes, more enlarged, from anaphases like the last; E, chondriosomes (at the same enlargement) from interkinesis of the larger spermatogonia (as shown in Fig. 1 A, B); F, very early spermatogonial anaphase (from rosette-cyst), with thread-like chondrioconts, Golgi-bodies (?) at the poles.

* In Fig. 3 C. the chondriosomes are represented slightly too large.

in each case, is a single and homogeneous substance or may consist of specifically different components; and the question may even be raised whether chondriosomes and Golgi-bodies (like chromosomes) may differ qualitatively among themselves. Such a possibility, certainly, should not be lost sight of, especially in case of the chondriosomes, because of their possible rôle in differentiation.

The foregoing considerations involve important issues relating to the nature and perpetuation of protoplasmic systems generally. Modern cytologists (and *a fortiori* cell-physiologists) have looked askance at particulate or pangenistic views of cell-structure in so far as these have involved the conception of protoplasm as a composite built up from protomeres or self-propagating units, whether visible or ultra-microscopical. Large concessions to such conceptions have been forced by researches on the nucleus, both cytological and genetical; but so far as the cytosome is concerned most recent researches, the present one included, have pointed in a different direction. The possibility nevertheless remains that cytoplasmic systems generally may include many different stuffs that are self-perpetuating by some kind of autocatalytic process.¹² We may venture the further surmise that such stuffs may undergo individuation in various degrees to produce visible formed bodies which in their fullest development became definitely organized as such and capable of self-perpetuation. Centrioles, for example, undoubtedly may perpetuate themselves by growth and division; yet it has been made extremely probable that under certain conditions they may also be formed *de novo*.¹³ It has been held that the same may be true of the plastids of plant cells, though this seems never to have been definitely proved.¹⁴ In case of the chondriosomes it would seem (if the results of Fauré-Fremiet are well founded) that the fragmentation of chondriosomes, though commonly irregular, has in some cases culmi-

¹² See Troland (1917).

¹³ Cf. Wilson (1901, 1925), Chambers (1921). See also experimental studies by Fry and by Tharaldsen now in press.

¹⁴ See Harper (1919).

nated in a regular process of fission, synchronized with mitosis.

Admittedly, the foregoing suggestions involve a somewhat preformistic conception of cytoplasmic systems; but it is one that differs widely, I think, from the intracellular pangenesis of Weissmann, Altmann and similar micromeristic hypotheses of other earlier writers. Should it prove well founded it might offer a more acceptable alternative to those speculative constructions—one that is more in accordance with modern views of protoplasm and comes more closely into touch with the problem of development. Experimental studies in embryology have clearly demonstrated the correctness of the early conclusion of cellular embryologists that the cytoplasm of the unsegmented egg contains specifically different, but not visibly formed, materials that are segregated in definite manner by the process of cleavage.¹⁵ Whether any or many of these are self-perpetuating is a question of far-reaching interest alike to the embryologist, the cytologist and the geneticist, and hardly less so to the biophysicist and the biochemist.

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¹⁵ See Wilson (1925).

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PARASITISM AMONG THE HELMINTHS¹

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INTRODUCTION

IN considering the parasitic helminths and their habits one is reminded of the popular presentation of the subject by P. J. van Beneden in "Animal Parasites and Messmates," which was of appealing interest to the naturalist of five decades ago. Since that time, however, the knowledge in this field has increased tremendously, although regrettably a considerable portion of the data deals with systematic classification and description of species. However, Schaudinsland, Leuckart, Looss and others, who worked on the life-histories of various forms, introduced the experimental method into the study of the groups and became the forerunners of the helminthology of the present day. The important rôle which many of the helminth species of man have been found to play in human disease in tropical and oriental countries has within recent times stressed that phase of the subject, perhaps to the disadvantage of the problem of parasitism among helminths as a physiological group, since it shifted the interest from the field of pure biology to that of an applied field. It is worth while, therefore, to pause for a few moments, and to consider the subject of parasitism among helminths as a whole, in the broader, more theoretical, but at the same time more fundamental sense, in order that one may reconsider the problems of a half century ago and may recast and reformulate theories on the basis of the data now in hand and the prospects immediately in view.

¹ Contribution from the department of medical zoology, School of Hygiene and Public Health, Johns Hopkins University, and the parasitology laboratory, Peking Union Medical College.

For practical purposes one may divide the parasitic helminths into two groups, namely, those belonging to the Platyhelminthes or flatworms, including Trematodes and Cestodes, and those belonging to the Nemathelminthes, or roundworms. Although it is not my purpose to discuss the classification of these groups, I shall present my subject as regards the trematodes, cestodes and Nemathelminthes first under separate headings, and then proceed to a general consideration of the phenomena attendant on parasitic adaptations among the helminths as a whole.

THE TREMATODES

The primitive development in the Trematodes was a direct one, with the larva as an important stage in development. (See text figure A). In the case of the ectoparasitic flukes, this type of development has not been materially or fundamentally altered, the only modification being that of a differentiation of the posterior part of the body of the larva into a holdfast organ for the purpose of attachment of the worm to the external tissues of the host (Plate I, fig. 2b). Thus the hermaphroditic adult produces ova in which the embryos develop to a certain stage when they escape from the egg shell, find a place of attachment for nourishment on the gills or in the bladder of the new host and, in turn, develop to adulthood.

In the case of the other group of trematodes, an endoparasitic existence must have become a fixed and obligatory condition early in their phylogenetic career. All lines of careful and weighed evidence point to the probability that the first host to which they became adapted was the mollusc. Some of the reasons for this belief may be stated as follows. (1) The mollusc is an invertebrate host, mainly adapted to an aquatic or moist habitat such as that favorable for the existence not only of the primitive trematode but of the present free-living relatives of the group (the Turbellaria). (2) The mollusc is a cold-

blooded animal with body fluids and tissues not essentially different in tonicity and nourishment content from those of the simple platode. (3) The first relationship of the trematode to the mollusc was undoubtedly an ectoparasitic one on the organs in the body cavity, particularly the kidney. The habitat of *Aspidogaster* and other *Aspidocotylea* is essentially this place to-day. As far as is known, the larva of this group reaches this position soon after its escape from the egg and here grows to adulthood (Plate I, fig. 2 c). (4) With the development of salivary glands for digesting of host tissues, a condition actually obtaining in certain aspidobothrids (l. c. *sg*) and elaborated very considerably in the digenetic trematodes, penetration of the molluscan host tissues was effected, where a source of nourishment as well as a comfortable place of residence was provided in the lymph spaces which bathe all the essential organs of the body. Gradually, the flukes became localized in the interhepatic lymph spaces and those surrounding the hermaphroditic organs of the mollusc, where a place of nourishment *par excellence* was provided.

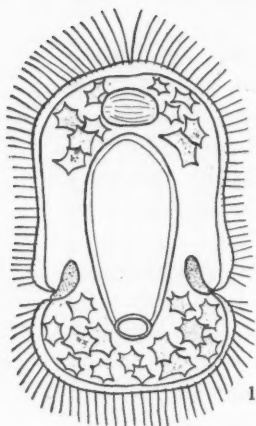
Between this essentially simple primitive condition of endoparasitism and that of the complex situation in the majority of digenetic trematodes, where one or more vertebrate hosts are involved, there is a very wide gap, which is represented in fact by various conditions of complexity, with modifications, elaborations, "short-cuts" and adaptations differing almost in every species which has come under investigation.

For convenience we may refer to the various stages in the life-cycle of the digenetic trematode as follows:

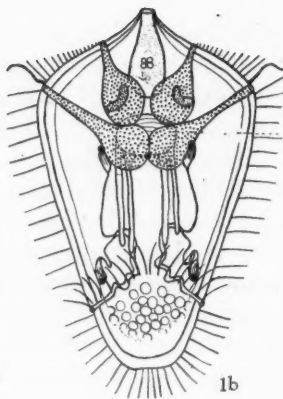
(1) The *miracidium*, or larva hatched from the fertilized egg (Plate I, fig. 1b).

(2) The *parthenita* (or parthenitic generation).² Parthenitae are those generations in the molluscan host in which reproduction is parthenogenetic and viviparous (Plate I, figs. 1c and 2d).

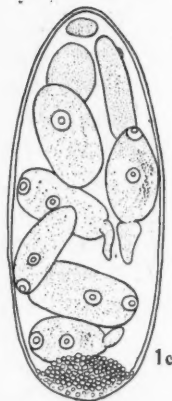
² The term "parthenita," now recognized by trematode investigators, was originally advocated by Sinitzin (1911), and introduced into the western literature by the present writer in 1918.



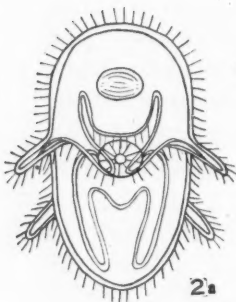
1a



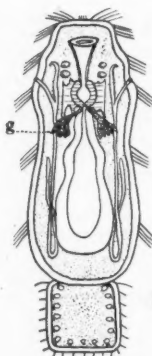
1b



1c



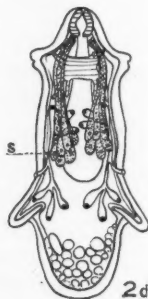
2a



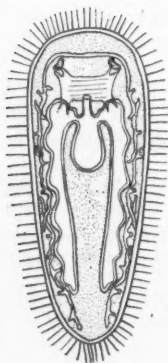
2b



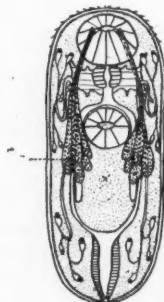
2c



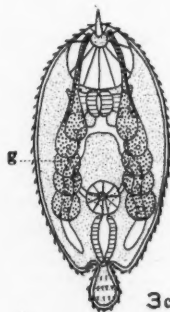
2d



3a



3b



3c

PLATE I. Typical stages in the development of Turbellaria and monogenetic and digenetic Trematodes, illustrating the kinds of modification effected with the assumption of a parasitic existence. 1a, young pilidium larva of a turbellarian (considerably modified from Lang); 1b, miracidium of bloodfluke, showing original adaptation to a free-swimming stage, with salivary glands for destruction of host tissue; 1c, sporocyst or metamorphosed miracidium (second generation) highly modified to meet the parasite life; 2a, Müller's larva, an indirect turbellarian type; 2b, larva of the ectoparasitic trematode, *Polystomum* (after Zeller); 2c, larva of *Aspidogaster conchicola* immediately after hatching; 2d, redia, or semi-modified parthenita of second generation; 3a, young planarian, having direct development; 3b, *Cercariaeum* or tailless Cercaria (modified from Cort); 3c, microcercous cercaria of *Paragonimus westermani*. (All drawings are original if not otherwise stated.)

(3) The *cercaria*, or tailed larva, which lives a free existence during transfer in those species having an active migration from the mollusc to the vertebrate host (Plate I, fig. 3c).

(4) The *adolescaria* (terminology of Ssnitzin, 1911),³ or agamestome stage, intermediate in maturity between the cercaria and the adult form in the vertebrate host.

(5) The *marita* (terminology of Ssnitzin, 1911) or sexually mature flukes in the vertebrate host. They are usually referred to as the "hermaphroditic generation," but this term is not sufficiently comprehensive, for it does not include such groups as the blood flukes in which the sexes are separate.

In general, it may be stated that there are examples of all these stages of development within the mollusc, but that functional parthenitae are not known for vertebrate hosts except in the case of certain monostomes, *Cyclocoelum mutabile* (Zeder) and *Typhlocoelum flavum* (Mehlis) in which each miracidium, which hatches from the egg while still in the uterus of the marita, contains a single well-formed redia or second generation parthenita. But here it is necessary for the miracidium to reach a molluscan host before further development can take place. A much more illuminating condition obtains in the case of *Cercaria indica* XV, a fork-tailed cercaria belonging to the non-mammalian group of blood-flukes, which has recently been described by Sewell (1922). In this species the miracidium metamorphoses into a parent sporocyst (first generation parthenita) which, in turn, produces daughter generation sporocysts parthenogenetically. These daughter sporocysts have the power of producing parthenogenetically both cercaria and miracidia (*l. c.*, pl. XXXII, figs. 1, 2). While the cercaria are able to seek a vertebrate host, the parthenicolous miracidia may reinfect the molluscan host already parasitized or may swim out of the mollusc and attack and infect other susceptible molluscs. Thus we have here a clue as to the complete life cycle involving both molluscan and vertebrate hosts, and, in addition, the remarkable condition in which the abbreviated life cycle may be completed without the interpolation of the maritic generation.

³ Dollfus's term "*metacercaria*," designating this stage, is neither based on sound morphological nor on genetic evidence.

We may describe the life history of a typical digenetic trematode in some such terms as these. The miracidium, which is furnished with a ciliated epithelium for a free-swimming existence, and which, likewise, has secretory glands for digestion of host tissue, by a specific tactile stimulus, possibly that of the mucus secreted by the mollusc, is attracted to a certain mollusc in its immediate neighborhood, drives headlong toward the mollusc and at the first point of contact pours forth histolytic ferments. If the enzyme is specific and this point of contact consists of soft tissue, then an entrance into the mollusc is effected. Gradually working its way inward, the parasite reaches the lymph spaces of the host and finally arrives at the interhepatic lymph sinuses.

Primitively, the larva escaping from the egg, as in the ectoparasitic trematodes, developed *in situ* into a hermaphrodite adult worm. But under the change of conditions as an endoparasite the genital complex has become simplified and parthenogenesis has been substituted, with the production of one or more daughter individuals. Usually, the miracidium (Plate I, fig. 1b) metamorphoses into an extremely simple organism, the sporocyst (Plate I, fig. 1c), in which only ectodermal and mesodermal layers are present and in which the endoderm has disappeared. There is a body cavity which serves as a brood pouch for the developing daughter embryos. These daughter individuals then grow to maturity, escape from the mother sporocyst, and, in turn, produce parthenogenetic young. But the second generation parthenitae consist also of simple organisms, either second generation sporocysts, as in the schistosomes or xiphidiocercariae, or of rediae, which are homologous almost part for part to the larvae of the aspidobothrids, with a definite axial gradient, and with well-developed pharynx and rhabdocoel gut. (Compare figures 2c and 2d). There follows a granddaughter generation,⁴ which may be an-

⁴ *Bucephalus* and *Leucochloridium* apparently omit the second generation of parthenitae and produce *Cercariae* within branched first generation sporocysts.

other generation of rediae (described for *Fasciola hepatica*) or even miracidia (in Sewell's blood-fluke), but which are most usually tailed larvae, the cercariae. Primitively, these larvae did not exist. Even where the vertebrate become involved as a host, no doubt the transfer was made passively, the flukes being taken over into the vertebrate along with the mollusc which served as food for the vertebrate. This situation prevails to-day in the case of *Aspidogaster conchicola*, in which the maritic adult has been found in the digestive tract of fishes (*Leuciscus aethiops*) and turtles (*Amyda sinensis*), as well as gasteropods and bivalves, in which it more usually develops. But a condition must have arisen in which there came to exist on the part of the fluke a "desire for more worlds to conquer," and to meet this need a larva capable for a brief period of a free-swimming existence was produced. Unlike the miracidium, this larva possessed no cilia, so that the locomotor function was effected by the development of a caudal appendage. Certain tailless larvae of the distome group, called *Cercariaea* (Plate I, fig. 3b), belonging to the same generation as cercariae, illustrate this more primitive condition.⁵ As in all other groups of animals the tail in some cercariae has become elaborated far beyond its functional justification and actually constitutes a burden to the larva. In other cases it has become modified to serve other functions.

The cercaria on reaching a suitable vertebrate host has one of two possible procedures. It may penetrate the tissues of the host or it may be taken in with the food of the host. To effect the former method of invasion salivary glands have been developed in the cercaria as in the miracidium (compare figs. 3b and 3c with 1b). The human blood flukes represent a group which still use the skin method of entrance effectively. But apparently most of the trematodes were not entirely successful with this

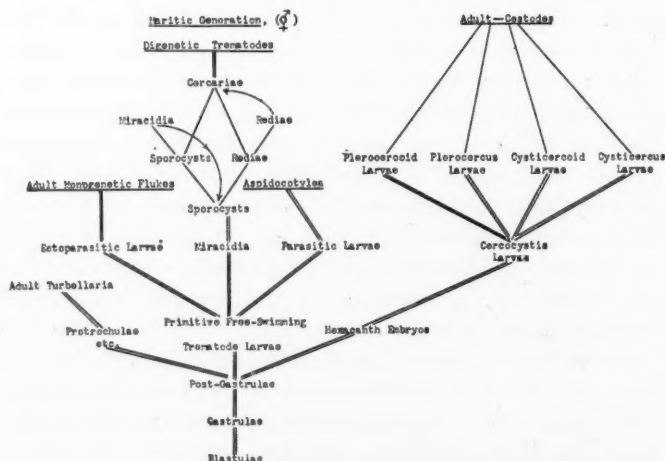
⁵ Ssinitzin (1911) claims that even the *Cercariaeum* has the rudiment of a tail in its embryonic stage.

method and there remained for them the alternative of inclusion in food material. Since the life of the cercaria as a free-swimming organism is ephemeral (it usually can not digest food), and since the cercaria can not pass the acid medium of the stomach of the vertebrate without being digested, it became necessary for a second type of glandular structure to become elaborated by the larva, namely, the cystogenous glands. These glands secrete an impermeable substance around the cercaria which effectively protects it against the unfavorable conditions of the environment, whether these be desiccation, hyperacidity or merely a long period of passive existence before the larva reaches its next host. In some cases, as in *Fasciola hepatica*, *Fasciolopsis buski*, many monostome, amphistome and echinostome larvae, encystment occurs on vegetable matter, which offers a satisfactory means of transfer to the digestive tract of the vertebrate. Such a parasite is able to accommodate itself to a considerable number of such hosts. Another group of cercariae is able to effect penetration of the epithelial and subdermal tissues of a vertebrate or arthropod previous to encystment. This host, in turn, becomes the food of another host (in every instance known, as amniote) and serves for the fluke's transfer to a place where it may mature. Thus, in the case of *Clonorchis*, *Loxotrema*, *Opisthorchis* and certain echinostomes and holostomes, fish serve as passive carriers of the adolescent fluke, while consumption of the fish on the part of birds or mammals, as the case may be, transfers the infection to the definitive host. In the case of *Paragonimus*, fresh-water crabs and crayfish replace the piscian host during the adolescent stage. Finally, there is a third type of encystment which takes place while the cercaria is still in the tissues of the mollusc, or even in the brood cavity of the parthenita itself. This last type is highly suggestive of the mollusc being the food of the next potential host.

The adaptation of the cercaria or encysted adolesearcia to the definitive host is more or less a fortuitous one. In

the case of the cercaria of *Schistosoma japonicum* or *S. haematobium* there is probably no active selection of the mammalian host. The cercaria is present in the water which comes in contact with the unprotected body of the mammal. When the mammal leaves the "infected water" and the surface layer of water begins to evaporate the cercariae attempt to bore into the tissues to keep from drying up. This is not peculiarly a reaction of larval trematodes but of certain nematodes (*Strongyloides*, hookworm, etc.) as well. If the effort is successful and penetration is effected, as in the case of mammals, further development is possible. *Clonorchis sinensis* has a wide range both of piscian and of mammalian hosts. *Fasciola hepatica* may become a parasite of any herbivorous mammal. Thus one finds that specificity of hosts in the digenetic trematodes has very little to recommend it as a theory, since the host secured is more or less dependent on factors both external and internal which control the situation for the parasite.

PLATYHELMINTH RELATIONSHIPS



Text Figure A. Scheme of phylogenetic relationship of the parasitic flatworms.

THE CESTODES

When one thinks of the cestodes or tapeworms he usually has in mind the multi-segmented ribbon-shaped worms which are commonly parasitic in the digestive tract of vertebrates. Such a form is commonly divided into "head," "neck" and "body." The "head" serves as a means of attachment, the "neck" constitutes the subapical undifferentiated region or potential growth area of the worm, and the "body" consists of immature, mature and gravid segments. The last mentioned parts are those found farthest distad.

From the point of view of parasitism as a whole and particularly that of the cestode group, this type of tapeworm must be regarded as a very highly specialized form, far removed from the more simple cestodes most nearly related to their free-living ancestors. With the cestodes, as with the trematodes, the free-living ancestor of the group is regarded as an offshoot of some form which was also the precursor of the Turbellaria. (See text figure A). This ancestor had a direct development, without metagenesis, and possibly also without even a larval stage in the strict sense of that term. Such a primitive condition exists to-day in the genera *Archigetes* (Plate II, fig. 4b) and *Caryophyllaeus*, where the development requires no cysticercus stage. That such an ancestral form was ciliated is fairly well proved by the ciliated ectoderm of several groups of cestodes of the present day. The primitive cestode may or may not have had a digestive tract. There is no evidence of such a system in cestodes to-day. Furthermore, it seems likely that if such a system ever existed in the group it was lost at an early period, since there is no evidence in the embryology of the group to warrant the belief that any of the primitive endoderm became differentiated into a digestive tube. Gastrulation is believed to occur by epibolic circumrescence at the animal pole of the egg, a ciliated or cuticularized ectodermal layer is developed, and the remaining endodermal cells remain as undiffer-

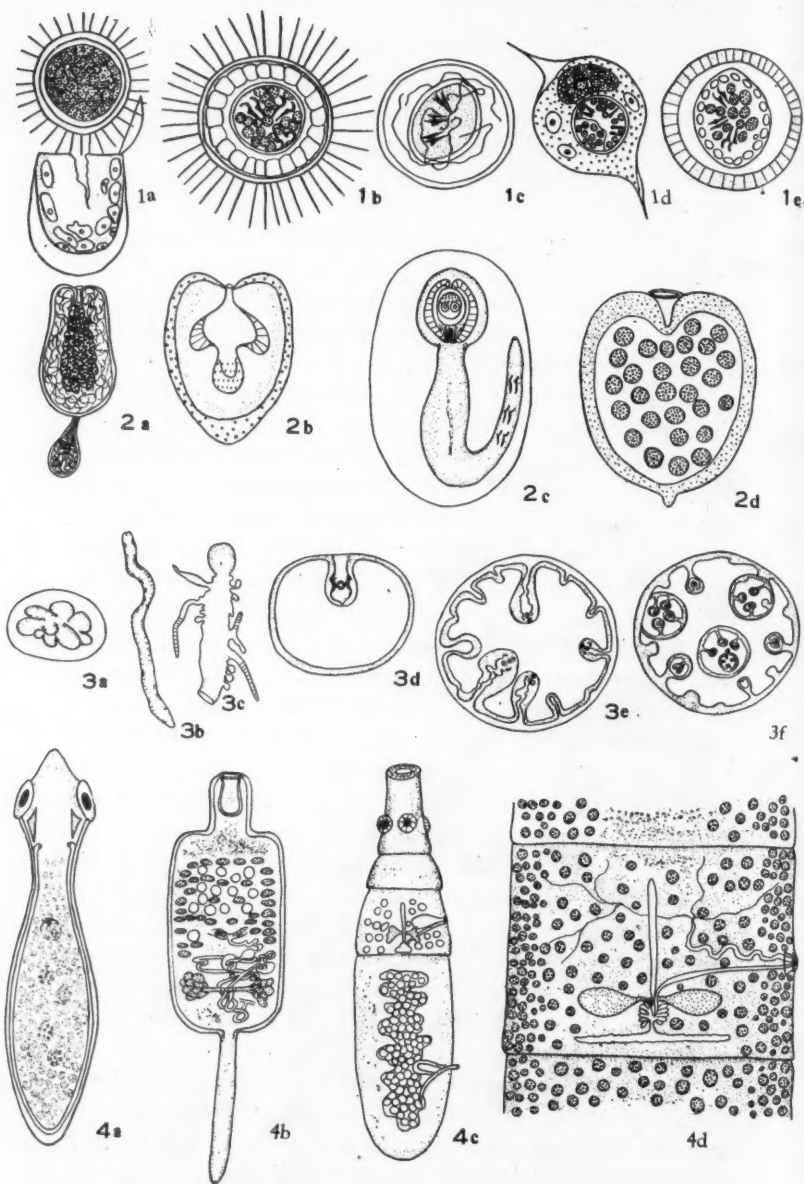


PLATE II. Typical stage showing the adaptation of cestodes to a parasitic existence. 1a, 1b, ciliated hexacanth embryos of *Diphyllbothrium latum* (after Rosen); 1c, hexacanth embryos of *Hymenolepis nana*, with polar filaments (after Stiles); 1d, 1e, hexacanth embryos of *Taenia saginata* (1d, immature, after van Beneden); 2a, procercoid of *Diphyllbothrium latum*, showing salivary glands (after Rosen); 2b, cercocystis (plerocercus) of *Dipylidium caninum* (modified from Leuckart); 2c, cercocystis (cysticercoid) of *Hymenolepis nana* (after Grassi and Rovelli); 2d, young cercocystis of *Taenia saginata* (after Leuckart); 3a, *Polycercus*, a primitive larva with exogenous budding (after Haswell and Hill); 3b, *Sparganum* (plerocercoid) of *Diphyllbothrium mansonii*; 3c, *Urocystidium gemmiparum*, showing exogenous budding and segmentation (after Beddard); 3d, cysticercus of *Taenia saginata*; 3e, coenurus of *Multiceps multiceps*; 3f, echinococcus or multiple hydatid; 4a, *Ilisha parthenogenetica*, a scolex larva (after Southwell); 4b, *Archigetes sieboldi*, a primitive cestodarian (after Mrazek); 4c, *Taenia echinococcus*, producing only one gravid and one mature proglottid at one time (after Leuckart); 4d, mature segment of *Taenia saginata*. (All drawings are original unless otherwise stated.)

entiated mesenchyme, except for the six cells which produce the hooks of the typical hexacanth embryo.

For the primitive parasitic cestodes only one host was required, probably an invertebrate. The egg was swallowed by the host, passed into the digestive tract, penetrated the wall of the mesenteron into the body cavity and there grew to maturity. However, some of these invertebrate hosts were food for vertebrates, so that before long two hosts, larval and definitive, were provided for the parasite. When such an alternation of hosts became obligatory, complications arose and the chances were very considerably lessened of the parasite completing its life cycle. To minimize this danger asexual multiplication was resorted to at two places in the life cycle, in the larva and in the adult. In the larval stage of the taenoid cestode, *Coenurus cerebralis* (Plate II, fig. 3e), in the brain of the sheep, a number of heads were budded off from the inside of the cysticercus. In the hydatid of hogs, sheep and man (Plate II, fig. 3f), not only daughter but also granddaughter heads are developed. Southwell and Prashad (1918) claim that *Ilishia parthenogenetica* (Plate II, fig. 4a) has met this difficulty by becoming a parthenita, but Woodland (1923) disputes this assumption. Recently, Professor O. Fuhrmann has shown me some of his unpublished researches in which he has demonstrated that the sparganum stage of the broad fish tapeworm, *Diphylobothrium latum*, also multiplies asexually within the musculature of the second intermediate host. Both budding and segmentation are described for *Urocystidium* (Plate II, fig. 3c). On the other hand, the adult cestode has become differentiated into an elongate ribbonlike structure, divided into segments, each one of which is sexually complete, and with a subapical region (the "neck") which possesses an almost unlimited capacity for further proliferation of such segments.⁶ Thus the number of segments proliferated is sometimes very great,

⁶ *Taenia echinococcus* (Plate II, fig. 4c) represents a condition in which only one gravid segment is produced at one time.

while the egg-production is enormous, so that the chances of miscarriage between hosts are more than compensated for by the overproduction of viable embryos.

In some cases among the higher taenoid cestodes there are two mammalian hosts, as for example, the dog and the pig, the dog and the sheep, the dog and the rabbit, the pig and man and the ox and man. In the case of *Taenia saginata* and *T. solium*, specificity of both larval and adult hosts obtains, although there are numerous cases of both in which the larval stage, commonly found in the non-human host, occurs in a similar location of man. In this connection the relation of man to Manson's Oriental tapeworm, *Diphyllobothrium mansonii*, is of unique interest. The reservoir hosts of this cestode are dogs, cats and their wild relatives. The cercocystis larva develops in *Cyclops leuckarti*, which arthropods are swallowed by frogs and snakes along with their food. There in the musculature the larva develops into the sparganum stage (Plate II, fig. 3b) and in due season is taken into the digestive tract of the definitive host. But man may become the host of either the sparganum stage or of the adult cestode. In the former instance the infected *Cyclops* is taken in with drinking water and sparganosis in man results, in which the muscles of the thigh and back become infected. In the latter instance man eats the infected frog or reptile and comes to harbor the adult worm in his intestinal tract.

Certain other cestodes of man and higher mammals require an arthropod invertebrate host. In *Dipylidium caninum* of the dog, cat and man, and *Hymenolepis diminuta* of the rat and man, a flea is utilized. But in *Hymenolepis nana* the cercocystis stage is believed to develop within the tissues of the digestive tract of the mammalian host, a condition indicative of a recent telescoping of the life-cycle.

Although the cestode is believed to have a common ancestry with the turbellarians and trematodes, it has developed along lines much more divergent from those

groups than they are from each other. Multiplication in the larval stage of the cestode is asexual; parthenogenesis obtains at no place in the life-cycle with the possible exception of the one species cited above. In the adult stage asexual multiplication is pyramided upon sexual multiplication. However, the end result in both the trematode and cestode groups is the same, namely, the multiplication of individuals along with the lessening of chances of completing the life-cycle due to the alternation of two or more hosts.

THE NEMATHELMINTHES

(Text figure B)

Any attempt to treat the nematodes and their relatives in a comprehensive way is met by almost insuperable obstacles. The group is extremely large, comparable to the insects in numbers of species. Specificity of habitat or host is highly accentuated. Judging from the number of genera and species now known and the ease with which new forms can be discovered, it seems likely that only a small fraction of the existing species have come under observation. The investigator of this phylum may be compared to a speaker on the platform of a tremendous amphitheater, filled to capacity, standing so that when he looks in any one direction he can view only a very small part of his audience.

When one considers the nemathelminthes from the standpoint of the parasitologist he is confronted with additional difficulties. One may discuss "parasitic roundworms" or "free-living roundworms," but neither subject is complete without the other. To be sure, there are genera, such as *Ancylostoma* and *Necator*, which are obligatory parasites during a part of their existence, or even groups, such as the *Acanthocephala*, all members of which are parasites, but the majority of parasitic species have relatives living a free existence in the water or in the soil.

Viewed as a group, the parasitic roundworms are found to be much less modified because of their parasitic exist-

ence than either the trematodes or the cestodes.⁷ Their adaptation has been much more easily accomplished and their life cycles much less complicated by alternation of generations or of hosts. Very few forms in the group possess a multiplicative period outside of the definitive host, and these are free-living generations of the life-cycle. If we are to believe the evidence presented by *Strongyloides*, it seems that in the free-living generation a facultative parthenogenesis exists. Both parthenogenesis and hermaphroditism are known for free-living species. However, the great majority of species depend exclusively on egg production in the adult parasitic generation for propagation. Certain parasitic nematodes are viviparous, as, for example, *Trichinella spiralis*, but similar instances obtain among free-living forms. The most interesting adaptation of the nematode ovum to a parasitic habitat is that of some of the *Filaroidea*, which live in the subcutaneous tissues, lymph spaces, or circulatory system of mammals. In *Filaria bancrofti*, which lives in lymph sinuses, the egg, usually passed into the circulatory system, is an elongate thread-like object spoken of as the filariform larva or microfilaria. In reality it is an elongate ovum, the shell of which is represented by the basal membrane covering the larva. Such larvae can pass the lymph capillaries and enter the circulatory system without difficulty, since the diameter of the larva is sufficiently small. But if the female *Filaria bancrofti* is traumatized or otherwise induced to lay immature eggs, these eggs being oval in shape can not pass the lymph capillaries, and, in part at least, are responsible for the lymph stasis which gives rise to lymphedema and elephantitis. A less advanced modification is found in *Dirofilaria immitis*, which lives in the right heart of the dog. In this species the eggs are usually laid in the immature mature (oval) stage, but develop to filariform larvae in the venous blood and later pass to the periph-

⁷ In this respect they are more comparable to the parasitic protozoa than to the parasitic flatworms.

eral circulation. In both cases it is necessary for the larvae to reach the peripheral circulation in order that they may be dispersed. *Dracunculus medinensis*, the guinea worm of Africa and parts of Asia, utilizes a much more primitive method of dispersal. The female worm wanders into a peripheral lymph space and at a favorable time and place bores a hole through to the surface of the skin. When this infected member of the host's body, particularly the hand or the foot, is immersed in water, the female worm, which apparently has a hydro-tactic reaction, utilizes this opportunity to oviposit. All these filarial nematodes require an intermediate arthropod host. In the case of the guinea worm, a *Cyclops* swallows the egg which the female worm has laid in the water, and is, in turn, swallowed in drinking water of the next host. The more highly adapted forms, however, require a transfer to be made through the bite of an insect host, in the case of *Filaria bancrofti* or *Dirofilaria immitis*, a mosquito, in the case of *Loa loa*, a mango fly. In either instance an incubation or developmental period is required in the insect, which later ejects the mature larva, which then penetrates the skin of the mammalian host. This life-history, and that of *Trichinella spiralis*, constitute the most radical modifications of the nematode parasite to its environment.

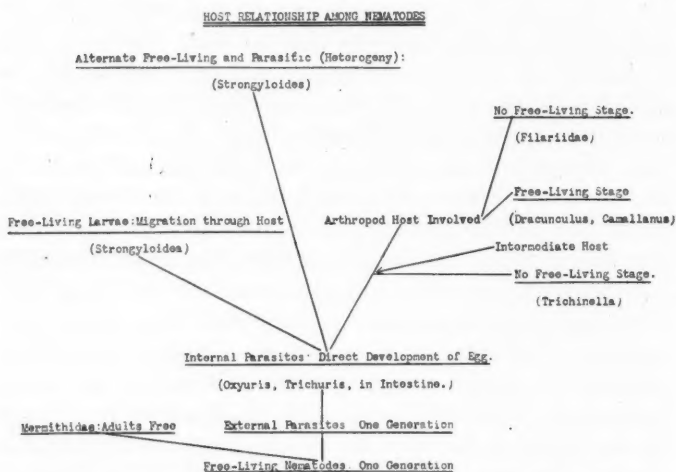
From the point of view of the entrance of the nemathelminth parasite into its definitive host, one may point out two possible routes of invasion, as in trematodes, the passive route into the digestive tract and the active route of migration through the skin. In the former instance, the eggs of the parasite may constitute a contamination of the food, which is the most usual method among the nematodes; or the larval nemathelminth, which has already become adapted to an intermediate host, may be taken into the definitive host along with the intermediate host, as is the case of all acanthocephala or thorny-headed worms in which the life-cycle is known. Some of these round worms taken into the digestive tract develop di-

rectly to adulthood, others undergo a migration through the tissues of the host before development can be completed. *Ascaris lumbricoides* is an example of the latter type. Whether this represents an old adaptation or a newly acquired accommodation is problematical. Another comparatively large group of nematodes actively enters the definitive host through the skin. As far as one is able to learn from the literature, the *Strongyloidea*, to which the hookworms, *Haemonchus contortus*, *Heligmosomum muris*, and related forms belong, all pass a free-living, post-embryonic existence, with one or more moults, and a change from a rhabditiform to a filariform larva (metamorphosis) and then ordinarily invade the definitive host through the skin. Likewise, the *Angiostomidae*, to which *Rhabdonema nigrovenosum* of the frog, and *Strongyloides* belong, after passing their free-living generation, all naturally invade their adopted vertebrate (definitive) host through the skin. Whether the route through the digestive tract, which small numbers of these larvae still survive, was the original method of invasion of the definitive host, still remains uncertain, but this is the most likely inference. The adaptation of the *Filaroidea*, whereby the larval stage became parasitic in Arthropoda, is a much more specialized condition of parasitism, in which both infection of the definitive host and dispersal of the worms is dependent on the arthropod. Only in the most highly specialized members of the family *Filariidae* does parasitism among the nematodes attain a degree of intimate dependence on the host which is so characteristic of the cestodes and the digenetic trematodes.

The *Mermithidae* and *Gordiaceae* are unique among parasitic nemathelminths in that the larval stage only is parasitic, usually in an arthropod host, whereas the adult individuals live a free existence, respectively, in the soil or water.

The *Hirudinea*, or leeches, and species of other groups constitute cases of parasitism more or less pronounced,

but in none of these groups has either the mode of life or the habitat caused such profound modifications to obtain as exist in the parasitic platodes or the more specialized filaroid nematodes.



Text Figure B. Scheme of host relationship among the nemathelminths.

GENERAL CONSIDERATIONS

When one has viewed the special groups of parasitic helminths with respect to their peculiar adaptations to the parasitic life, it is altogether fitting that certain of these phenomena be considered in the large, in order that the common trend of parasitism in metazoan invertebrates may to some extent be measured.

The subject under discussion confines one to the consideration of parasitism among helminths as viewed from the standpoint of the parasite and not of the host. As in the case among other groups of parasites an optimum condition for the parasite is one in which the number of parasites involved, their position in the host, and the secretions or excretions of the parasite do not set up a sufficiently grave pathological condition of the host to

endanger its life.⁸ For example, the presence of a dozen hookworms in the intestine of the host is not a matter of concern, for there are little or no clinical effects from such an infection. However, the wanderings of *Ascaris* into the liver, of *Paragonimus westermanii* or echinococcus into the ventricles of the brain, or the obstruction of an important lymph channel by a filaria may set up grave symptoms which endanger both the life of the host and of the parasite. Yet the establishment of optimum conditions for the parasite is entirely outside the powers of the parasite. Likewise, the number of individuals which completes a life cycle depends on many external factors entirely outside the control of the parasite, except as an indirect compensation is afforded by the influence of these unfavorable conditions in modifying the course of events, or the organic structure of the parasite. Thus the number of schistosome larvae entering a mammalian host is no direct index of the number which will reach the mesenteric-portal system, since fortuitous distribution through the lymphatic and circulatory systems condemns a large share of them to blind passages, there to die as foreign-body emboli within the host.

Nevertheless, it must be admitted that the majority of parasitic platyhelminths and nemathelminths have achieved unusual success in meeting the conditions of their parasitic existence. Perhaps the most extraordinary part of this whole adventure is the ability of many helminth parasites to live at one and the same time as parasites of warm-blooded vertebrates, together with a free-living existence or a parasitic life in an invertebrate host. The adaptation to differences in temperature, tonicity and chemicals in solution in the medium is even more of an achievement than the morphological changes due to differences in food supply or the elaboration

⁸ Some investigators regard this view as teleological. The adaptations of the helminth to the acid medium of the third and fourth stomachs of ruminants and their active resistance to host secretions may be easily demonstrated. An anesthetized but living helminth is soon digested in the same habitat in which it lives normally.

of acetabula and hooks for attachment to the tissues of the host.

Perhaps one of the most interesting problems involved in a study of the helminth parasites is that of host selection. Primitively, many of these relationships must have been mere fortuitous contact of parasite with host, but as adaptations became more and more intimate there have come to be definite correlations in some instances and definite satisfactions in others.

As an example of the former type one needs only to cite the relationship between the trematode miracidium and the mollusc. Undoubtedly this host selection on the part of the miracidium was originally a chance undertaking. It was mere accident as to what mollusc the miracidium would attack. Many species of miracidia are known to attack molluscs without successful penetration. Certain species of molluscs are more commonly found in certain habitats than others. The constant association of miracidia of one species with certain species of molluscs in this same habitat has brought about not only a tactic response of the larvae for such hosts, but also a specificity of cytolytic substance in the secretory glands of the larva which permits it to destroy or digest away molluscan tissue, and thus gain an entrance to the lymph spaces of that host. Thus the miracidia of *Schistosoma japonicum* have become adapted to the amphibious triculid *Rissoidae*, which enter only the surface stratum of the water, while the miracidia of *S. haematobium* and *S. mansoni* utilize an entirely different group of snails, the planorbids, which are much more cosmopolitan in their distribution and have entirely different edaphic requirements. Undoubtedly the confinement of schistosomiasis japonica to China, Japan, Formosa and portions of the Philippines is associated with the geographic distribution of the molluscan hosts utilized, else why has not the disease become established in Korea, Cochin-China, the Malay and other centers where human carriers are plentiful and where the climatic conditions

are favorable, but where the particular genera of molluscs are not found?

In the second instance, the process by which cercariae of the schistosomes and the filariform larvae of the *Strongyloidea* effect penetration of the definitive host is worthy of note. In either case there are probably three factors involved, namely, moisture, temperature and chemical stimuli. In both groups, all that is necessary to effect an attack and attempted penetration of the host tissue is to place the larvae in a drop of water on the surface of the body and allow evaporation to take place. If the adaptation is specific, penetration is effected. If it is non-specific, in the case of schistosome cercariae, a dermatoid rash is at least indicative of the attempt. Some four years ago I tried out this idea by placing on my forearm a drop of water covering an area the size of a penny, containing a number of *Cercaria leptoderma*, a non-mammalian blood fluke, at times found in the edible snail in the vicinity of Peking. In the course of a half-hour the water evaporated, accompanied by a definite itching of the area and the development of a definite erythematous rash. After two hours or so the rash disappeared, while the cercariae evidently failed to secure a penetration, since no untoward consequences were later experienced. In the case of nematode larvae normally entering the host via the skin Professor F. Fülleborn has shown that they will enter any tissue in the vicinity if the free moisture of the immediate environment is withdrawn. Slight increase in temperature in all these examples, such as that effected by placing the larva on the surface of a warm-blooded animal, stimulates activity. Information on the chemotactic response of the larva for the definitive host is as yet almost entirely wanting and should be investigated. Once the larva has reached the definitive host, there is again the matter of actual penetration to be accomplished. This involves either the elaboration of an enzymatic ferment specific for digestion of the host tissues through to the peripheral circu-

lation, or organs for mechanical abrasion and penetration, or both, and the degree of success is directly measured by the efficiency of these organs. Larvae which have not perfected these organs are unsuccessful in their efforts to effect penetration. The Oriental blood-fluke, which is potentially a parasite of all mammals exposed to the cercarial stage, is not found in the water buffalo in infected areas in China, not because the animal is immune to the disease but because the skin of the animal is too tough for penetration, whereas the native cow harbors the infection.

There is, however, a certain immunity to many helminth parasites, acquired as the host grows older. This problem has not been studied in detail, but it is known that on equal exposure children are more heavy carriers of hookworms, ascarids, whipworms, hymenolepids, etc., than are adults. Likewise, the chicken ascarid, *Ascaridia perspicillum*, is commonly "lost" by the chicken after a certain period of its life. This phenomenon is probably closely bound up with the formation of immune bodies in the host which overbalance the adaptations of the parasite for its host. In many cases there is a maximum number of helminth parasites of any one species which a host will harbor. This is apparently due to a stimulation of the host on the part of the parasite, whereby the host is able to throw off hyperinfections. That the phenomenon is due to some substance fabricated by the parasite is demonstrated by the fact that saline extracts of the parasite, when injected into the host, will frequently not only prevent additional infections but will at times cause the host to lose its original infection.

INCREASE IN EGG WEIGHT IN RELATION TO THE TIME THAT LAYING COMMENCES

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THE standard method of measuring the laying capacity of a pullet is the number of eggs laid during what is termed the pullet year of production, but it is possible that there are means of determining in advance of the conclusion of the laying year the potential producing capacity of a pullet. Hadley (1919), for instance, has developed the thesis that increase in egg weight serves as a criterion of numerical production and that it is possible to determine in advance of the conclusion of the first year of production the relative potential laying capacity among individuals in a flock of pullets.

The theme of immediate interest in this paper is a critical analysis of the results secured by Hadley in a study of egg weight in relation to production in a flock of 38 white Plymouth Rocks at the Rhode Island Experiment Station, inasmuch as the results are not in entire agreement with those secured by the writer in his study of the same problem in a flock of 60 barred Plymouth Rocks at Macdonald College. Furthermore, it is apparent, as discussed below, that in the treatment of his data, Hadley overlooked one important factor, which if taken into consideration probably would have altered materially the conclusions drawn.

The 38 white Plymouth Rocks were hatched in April, 1909, and are reported by Hadley to be of equal age and condition, presumably at the time laying commenced. He does not say when his birds commenced laying, and this is a very important point, inasmuch as it has been observed, Lippincott (1921), Atwood (1923) and Jull (1924), that there is a very significant correlation between age in days laying commences and the mean

weight of the first ten eggs laid. It is unfortunate, therefore, that Hadley made no record of the month that laying commenced, and the importance of this matter will be emphasized later in dealing with the factor of increase in egg weight in relation to production.

What Hadley apparently failed to realize was that the time that laying commences is a very important factor affecting the mean weight of the first ten eggs laid. This point is clearly demonstrated by reference to Figure 1. Since Hadley has treated his matter on a monthly basis,

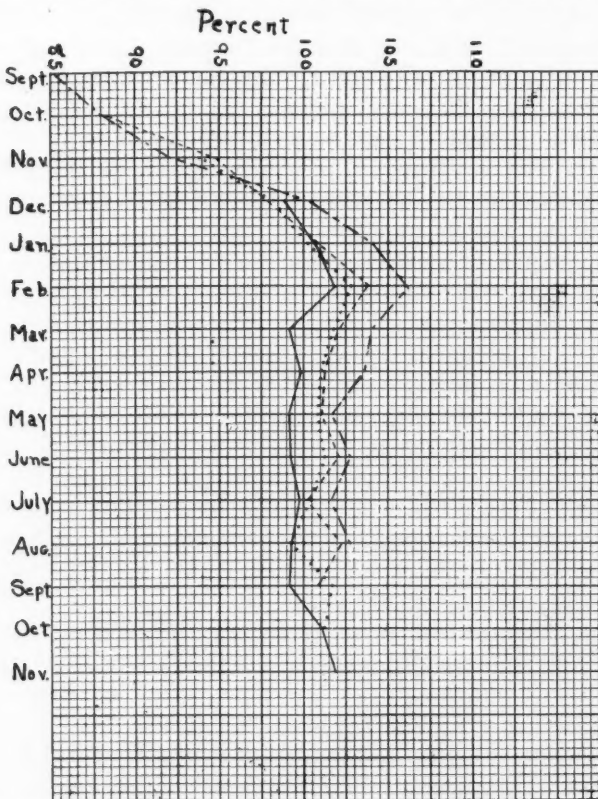


FIG. 1. Showing the monthly mean egg weights as percentages of the mean egg weights of the total production, according to the month laying commenced.

the writer has done the same, in order that the results might be comparable. It has been pointed out previously that several investigators have demonstrated the existence of a high and significant correlation between age in days laying commences and the mean weight of the first ten eggs laid. It would be expected, therefore, that the first ten eggs laid by birds commencing to lay in September would be considerably lower in mean weight than the first ten eggs laid by birds commencing to lay in December, providing all the birds were hatched about the same time.

Among the 60 birds, 17 started to lay in September, 10 in October, 16 in November and 17 in December. The eggs were weighed daily as laid, with the exception of eggs laid on Sundays, holidays and occasionally other days. The mean weight of the total annual production as well as the mean weight for each month were determined in the case of every bird. When the monthly mean egg weights for each group of birds, according to the month laying commenced, are expressed as percentages of the mean egg weights of the total production for each group and are plotted on monthly ordinates, as shown in Figure 1, the point is brought out clearly that the earlier in the season that laying commences the smaller are the first eggs laid in relation to the mean weights of the total production. From this it naturally follows that the earlier in the season that laying commences the greater would be the increase in mean egg weight of ten eggs laid in April or September over the first ten eggs laid.

In the case of the 38 white Plymouth Rocks the egg-weight curve was of a bimodal type, one mode occurring in April and one in September. In the case of the 60 barred Plymouth Rocks the egg-weight curve shows one mode only, which occurs in February. That is, in the flock of 60 birds monthly mean egg weight increased up to and including February and then it gradually decreased. It may be said that ten eggs about the middle of February were selected because February was the modal month of monthly mean egg weight, just as April

and September were the modal months of monthly mean egg weight in Hadley's work.

In order to compare the April mean egg weight with the mean weight of the first ten eggs, Hadley divided his flock into two groups, one group comprising the birds which laid more than the flock mean of 120.00 eggs and another group comprising the birds which laid less than the flock mean. The first group had a mean production of 143.00 eggs and the mean percentage of increase in mean egg weight was 5.40 per cent. The second group had a mean production of 99.00 eggs and the mean percentage of increase in mean egg weight was 2.60 per cent. Not as many birds were laying in September as in April, and when the flock was divided on the same basis the group of birds, each laying more than the flock mean, had a mean production of 151.00 eggs and the mean percentage of increase in mean egg weight was 5.80 per cent., while the group of birds each of which laid less than the mean for the flock had a mean production of 105.00 eggs and the mean percentage of increase in mean egg weight was only 1.00 per cent. The writer divided his flock into two groups, the first comprising the birds which laid more than and the second comprising the birds which laid less than the flock mean of 152.40 eggs. The February mean egg weight was compared with the mean weight of the first ten eggs laid. The first group, 34 birds, had a mean egg production of 178.54 ± 2.18 , and the mean percentage of increase in mean egg weight was 12.75 ± 1.06 . The second group, 26 birds, had a mean egg production of 118.31 ± 3.59 and the mean percentage of increase in mean egg weight was 8.31 ± 1.66 . The results obtained by the writer are in general agreement with those obtained by Hadley and seem to show that the birds with the greatest percentage of increase in mean egg weight were the birds that laid the greatest number of eggs. On the other hand, in a further examination of the results secured by the writer, it is observed that the difference in production between the first and second group is 60.23 ± 4.20 , while the difference in mean per-

centage of increase in mean egg weight is 4.44 ± 1.96 . The difference in production is highly significant, while the difference in respect to mean egg weight is not significant. Furthermore, when the month that laying commenced is taken into consideration it is found that in the first group 12 birds commenced laying in September, 6 in October, 9 in November and 7 in December, while in the second group 5 commenced laying in September, 4 in October, 7 in November and 10 in December.

Hadley next considered the relationship of the mean weight of ten eggs selected as closely as possible to the periods of absolute April and September maxima, respectively, to the mean weight of the first ten eggs laid. In both cases he divided his flock into two groups, the first group comprising those birds which showed an increase of 6 per cent. or more in the mean weight of the April and September ten eggs, respectively, over the mean weight of the first ten eggs laid, and the second group comprising those birds which showed an increase of less than 6 per cent. or a decrease. For April, there were 13 birds that showed an increase in mean egg weight of 6 per cent. or more and their mean annual production was 138.00 eggs, while there were 24 birds with an increase of less than 6 per cent., or a decrease, and their mean annual production was 114.00 eggs. For September, in the first group, there were 12 birds, with a mean annual production of 139.00 eggs, while in the second group there were 19 birds, with a mean annual production of 112.00 eggs. In order to secure results for comparison with those of Hadley, the writer determined the percentage of increase in the mean weight of ten eggs laid as nearly as possible around the middle of February over the mean weight of the first ten eggs laid. On this basis of consideration there were 38 birds that showed an increase in mean egg weight of 6 per cent. or more and their mean egg production was 155.89 ± 3.42 , while there were 22 birds that showed an increase of less than 6 per cent., or a decrease, and their mean egg production was 146.45 ± 6.95 . Here again the results are in general

agreement with those obtained by Hadley, but the difference in mean egg production is 9.44 ± 7.74 , which is not significant. Moreover, if the birds of the two groups are classified according to the month laying commenced, it is found that in the first group 17 commenced in September, 10 in October, 8 in November and 3 in December, while in the second group there were none that commenced in September, none in October, 8 in November and 14 in December. This suggests quite clearly that a division of the flock according as the mean percentage of increase in mean egg weight is more or less than 6 separates fairly completely the birds that commenced laying early from the birds that commenced laying late.

It is necessary to test further the matter of increase in mean egg weight in relation to production according to the month laying commenced, and for this purpose the results are shown in Table I. The column "Mean Percentage of Increase in Mean Egg-weight" refers to the percentage of increase in the mean weight of ten eggs laid as nearly as possible around the middle of February over the mean weight of the first ten eggs laid.

TABLE I
SHOWING THE MEAN EGG PRODUCTION AND THE MEAN PERCENTAGE INCREASE
IN MEAN EGG WEIGHT ACCORDING TO THE MONTH
LAYING COMMENCED

| Month laying commenced | No. of birds | Mean egg production | Differences | Mean per cent. increase in mean egg weight | Differences |
|------------------------------|--------------------|------------------------|------------------|---|-----------------|
| September | 17 | 153.00 ± 4.59 | 7.60 ± 7.32 | 23.00 ± 0.87 | 8.28 ± 1.43 |
| October | 10 | 160.60 ± 5.59 | 7.80 ± 9.27 | 14.72 ± 1.14 | 7.80 ± 1.50 |
| November | 16 | 152.80 ± 7.40 | 6.21 ± 10.57 | 6.92 ± 0.98 | 6.30 ± 1.38 |
| December | 17 | 146.59 ± 7.55 | | 0.62 ± 0.98 | |

From Table I it is apparent that the differences in mean egg production, according to month laying commenced, are not significant, and it may be added that the difference between the October group, showing the high-

est mean egg production, and the December group, showing the lowest mean egg production, is 14.01 ± 9.39 , which is not significant. The fact is borne out, therefore, that in this group of birds there is no significant correlation between month laying commenced and annual production. It is apparent, however, that the differences in mean percentage of increase in mean egg weight, according to month laying commenced, are significant in every case, and it may be added that the difference between the highest, September, and the lowest, December, values is 22.38 ± 1.31 , which is very significant.

This situation demonstrates that percentage of increase in mean egg weight is a far more significant criterion of the approximate time laying commences than it is of numerical production. This particular point is borne out very clearly by reference to the coefficients of correlation which have been determined. The correlation between egg production and percentage of increase in mean egg weight, 0.157 ± 0.085 , is positive but is not significant, and Hadley failed to demonstrate the significance of his apparent correlation. Between month laying commenced and egg production there is a slight minus correlation, -0.007 ± 0.087 , but it is not at all significant. On the other hand, between month laying commenced and percentage of increase in mean egg weight there is a very high correlation, 0.911 ± 0.015 , and it is very significant. There can be no question, therefore, that time laying commences is a very important factor affecting increase in mean egg weight and it is very unfortunate that Hadley did not take the question of time laying commenced into consideration.

In conclusion, it may be said that increase in mean egg weight can be considered a criterion of numerical production only in so far as time laying commences is a criterion of numerical production. Furthermore, it is highly probable that as a possible criterion of numerical production increase in egg weight is of an incidental character.

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A COMPARATIVE RACIAL STUDY OF THE STRUCTURAL ELEMENTS OF HUMAN HEAD-HAIR

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FROM recent studies of the structural units of the hair of mammals below the *Hominidae*¹ it has been shown that these units are characteristic rather of the diameters of the hair shafts in which they occur than of the species of mammals bearing the hair. With respect to the structural parts of the outermost integument of the hair-shaft, *i.e.*, the cuticular scales (Fig. 1), it was found that the scale-forms, as expressed by the *scale-index* (a mathematical expression of the relationship between the proximo-distal diameter of the free surface of the scale and the diameter of the hair-shaft (Fig. 3)) bore relation, not to the species, nor to the group to which it belonged, but to the size of the hair. Without using the terms in their strict mathematical sense we may say that the width of the cuticular scales and the diameter of the hair shafts vary inversely. Or, roughly, the coarser the hair, the finer the scales; and *vice versa*.

It was further found that the forms assumed by the medulla, the central column of cells of the hair shaft (Fig. 5) likewise vary with the diameter of the hair shaft, in a similar way.

Scale and medulla form are thus shown to be intimately related to the diameter of the hair shaft, in a general way. Specific and group characteristics of the minuter configurations in these two structural elements exist, however; characteristics of sufficient magnitude and definiteness to be useful to the trichologist.²

¹ Hausman, L. A., "Further studies of the relationship of the structural characters of mammalian hair," *AM. NAT.*, Vol. 58, Nov.-Dec., 1924, p. 544.

² *Ibid.*, "Structural characteristics of the hair of mammals," *AM. NAT.*, Vol. 44, Nov.-Dec., 1920, p. 496.

The cortex of mammalian hair seems to be quite uniform throughout the class and consists of elongated, shrunken cells, whose keratized cytoplasm frequently exhibits traces of nuclei. This whole element of hair-shaft structure is usually an almost homogeneous and hyaline mass.

The pigment granules, both of the cortex and the medulla, are deserving of much study. In the *infra-hominid* mammals many specific differences with respect to their color value, hue, size and placement obtain.³ Studies of the pigment granules in human head-hair are being carried on in the writer's laboratory.

The hitherto unsuspected relationships between the hair-shaft diameter and its structural units, which the studies just mentioned have revealed, suggested that similar investigations be undertaken of the status of these same elements in the head-hair of the various races of mankind. Accordingly, a collection of scalp-hairs representative of all the existing races of man was made from various sources⁴ and a comparative study of the struc-

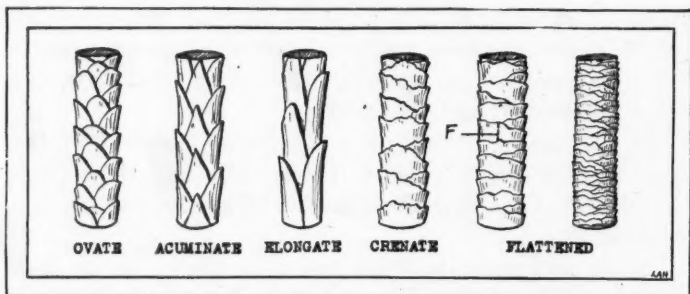


FIG. 1. The five types of imbricate cuticular scales of mammalian hair. (The coronal scales, not shown, form a distinct group.)⁶ The figure on the extreme right is of a portion of a shaft of a typical human head-hair. At F is shown the method of measuring the proximo-distal diameter of the free surface (i.e., the width) of the scales.

³ *Ibid.*, "Hair coloration in animals," *Sci. Mon.*, Vol. 12, March, 1921, p. 215.

⁴ The writer is greatly indebted to the following persons for the samples of head-hair they have sent him, and heartily thanks them: First, and especially, Dr. Aleš Hrdlička, of our National Museum in Washington; Dr. Chi

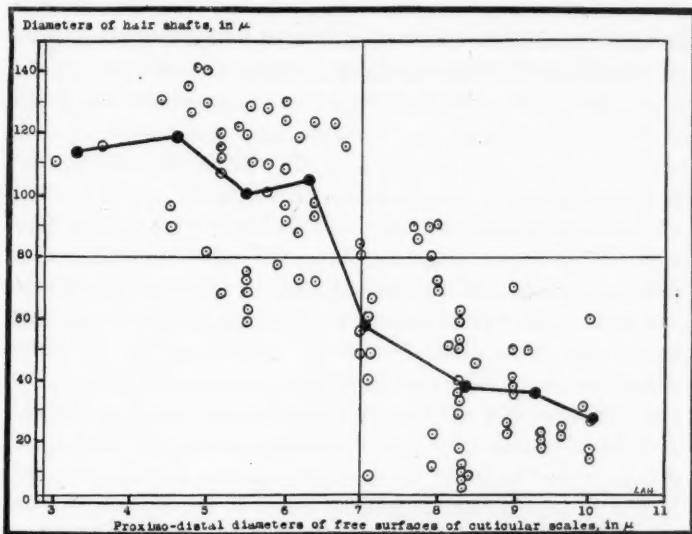


FIG. 2. Relationships between the sizes (*i.e.*, widths, or proximo-distal diameters of the free surfaces) of the cuticular scales and the diameters of the hair-shafts, as shown in 94 specimens of human head-hair from individuals representing all the existing races of mankind.⁷ Clear circles represent the individual data. The determinations were made, in each case, midway between the base and the tip of the hair-shaft.

tural elements made. The results of the studies of the cuticular scales and medullas are here presented.

The earliest comprehensive microscopic study of human hair was made by Pruner-Bey in 1863 and 1864.⁵

Ping, of the National Southeastern Teachers' College at Nanking; Dr. Arnold E. Lundie, of Idutywa, Cape Province, South Africa; Professor E. W. Stafford, of the Mississippi College; The Metropolitan Museum of Art, for a splendid series of mummy hairs from Egypt; Dr. T. C. Nelson, of Rutgers University; Dr. H. D. Reed, of Cornell University; Dr. A. L. Kroeber, of the University of California; and Dr. F. G. Speck, of the University of Pennsylvania, and many others.

⁵ Pruner-Bey, "De la chevelure comme caractéristique des races humaines, d'après des recherches microscopiques," *Memoires de la Société d'Anthropologie de Paris*, Vol. 2, 1863, p. 1; and *Deuxième Serie d'Observations sur la Chevelure*, *ibid.*, Vol. 3, 1864.

A general micrological survey of the hairs of men and beasts was made in 1884 by W. Waldeyer, in his "Atlas der Menschlichen und Tierischen Haare, etc." (Lahr). A copy of this work was kindly presented to the writer by Mrs. John A. Roebling, of Bernardsville, N. J.

He is chiefly to be remembered by his discovery of the relation between the trans-section of the hair and its degree of curliness. He recorded the fact that the more curly the hair, the more elliptical was its cross-section; and the more nearly straight the hair, the more nearly circular its cross-section. He noted that the thinnest and flattest hairs are those of the Bosjemans, Papuans and Negroes; and the most cylindrical those of the Polynesians, Malays, Thibetans, Siamese, Japanese and American Indians and Eskimos. Pruner-Bey also recorded his observations on the variability of the medulla-forms in various hairs, but was unaware of the relationships of these forms to the shafts in which they occurred. Supposing these differences in form to be constant, with relation to groups of peoples, he proposed that hairs should be classified on the basis of the medulla-status, as follows: (1) Hairs in which the medullary canal is empty of all substance, (2) hairs in which the canal is filled with substance and frequently terminated in the shaft, and (3) hairs in which the canal is absent altogether. The first form is the present writer's *continuous medulla*, and the second form, the *fragmentary, fractional and broken medullas* (Fig. 4).

The cuticular scales of human head-hair are all of the flattened type,⁶ and like the scales of the *infra-hominid* hairs (Fig. 1) vary, in a rough way, inversely with the diameter of the hair shaft. Fig. 2 shows graphically the relationships between the width (*i.e.*, the proximo-distal diameter of the free surface) of the cuticular scales and the diameter of the hair-shafts of ninety-four specimens of hair, representing the existing races of mankind.⁷

⁶ A classification of the cuticular scales of mammalian hair will be found in Hausman, L. A., "Structural characteristics; etc.," footnote 2.

⁷ The following ethnographic classification has been used by the writer, and is to be regarded by the reader, not otherwise than as merely a convenient check-list:

I. European Race.

- (1) South Mediterranean Branch
- (2) North " "

II. African Race

- (1) Negrillo Branch
- (2) Negro "
- (3) Negroid "

This is significant, for it means that the scale-forms are, therefore, unrelated to race. For it was found that the scales varied on contemporaneous hairs from the same head, and on hairs from the same head at different periods of life, when the diameters of these hairs varied. Moreover, differences exist along the same hair, from base to tip. This is interesting, in view of the fact that many *infra-hominid* hairs show this characteristic very much more markedly. An extreme instance of this change in character from the base to the tip of the hair, involving not merely the cuticular scales but the other elements of the shaft-structure as well, is furnished by the protective or over-hair of the Platypus (*Ornithorhynchus anatinus*).⁸ Such changes are explainable from the behavior of the epidermal cells at the base of the hair follicle. When a hair is about to be shed,⁹ the papilla atrophies, and the bulb of the hair becomes cornified and hard. Growth ceases, and the hair-shaft is carried outward toward the mouth of the follicle by the continued proliferation of the cells of the root-sheath. A new papilla now develops, and soon becomes surrounded by the cells forming the bulb of the new hair. The early proliferation of the cells forming the tip of the new hair produces a shaft of less diameter than that which succeeds, and which is the product of the increasing mitotic activity of the hair cells. When the papilla begins to atrophy, the shaft of the hair becomes smaller. Hence hairs very frequently show a narrow or even pointed tip, a broader middle portion, and a narrowing base. The

III. Asiatic, or Mongolian, Race

- (1) Sinitic Branch
- (2) Sibiric "

IV. American Race

- (1) Northern Branch
- (2) Central "
- (3) Southern "

V. Oceanic Race

- (1) Negritic Branch
- (2) Malayic "
- (3) Australic "

⁸ Hausman, L. A., "A micrological investigation of the hair structure of the *Monotremata*," *Am. Jour. Anat.*, Vol. 27, No. 4, Sept., 1920, p. 463.

⁹ Unna, P. G., "Beiträge zur Histologie u. Entwicklungsgeschichte der Menschlichen Oberhaut," etc., *Arch. f. Mikro. Anat.*, Vol. 12, 1876, p. 665.

average life of a continuously growing hair in the human scalp (that is, the period during which there is uninterrupted mitosis of the hair cells at the base of the follicle) is said to be between five and six months.¹⁰

Fig. 3 shows the relationships between the scales and the hair-shaft diameters as revealed by an examination of 185 species of *infra-hominid* hairs.

The human head-hairs show but one type of scale, as has been said, the flattened type. This is interpreted as being the cuticular scale indication that mankind is a single species. No differences in this type of scale, analogous to the specific differences to be found in the *infra-hominid* hairs, were encountered.

The medullas of human head-hairs varied also, but, like cuticular scales, not with race, but with diameter of hair-shaft. Fig. 4 records the results of the study of 122 specimens of head-hair, representing the five races of our table.⁷ The greater number of the finer hairs lack rather

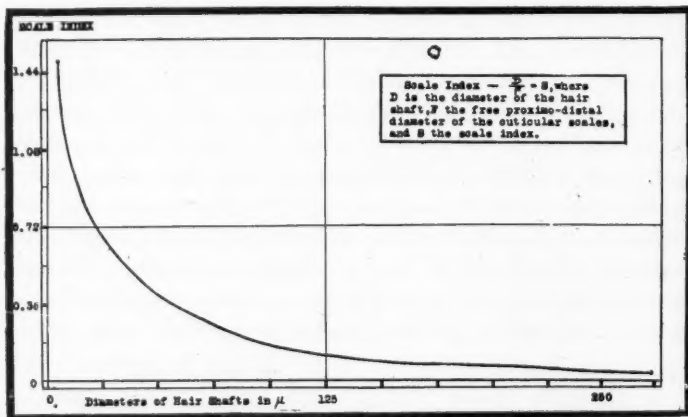


FIG. 3. Relationships between the sizes (*i.e.*, widths, or proximo-distal diameters of the free surfaces) of the cuticular scales and the diameters of the hair-shafts, as shown in 185 species of mammals below the *Hominidae* and representing all the existing orders except the *Cetacea*. The scale index, here recorded, is simply an expression of the ratio between the width of the scale and the diameter of the hair-shaft. The determinations, in each case, were made midway between the base and the tip of the hair-shaft.

¹⁰ Stöhr, Text-book of Histology.

than possess a medulla; and the greater number of the coarser hairs possess one rather than lack it. Intermediately sized hairs bear the various types of fragmental medullas shown in the figure. The relation between medullas and hair diameters among the *infra-hominid* mammals is shown by Fig. 5.

It is interesting and significant from the standpoint of what has been said regarding the close parallelism between both scale and medulla form and diameter of the hair-shaft to note what a comparison of these two curves reveals: (1) That in both groups the hair-shafts of about 100 microns in diameter bear virtually the same type of medulla and (2) that the *hominid* hairs do not show the *discontinuous* or *intermediate* types exhibited by the *infra-hominid* species.¹¹ From a series of studies of the finest hairs of very young children and of the hairs of the lanugo (hairs ranging in diameter from 10 to 30 microns) it was found that in the great majority of cases the medulla was absent. It is noteworthy, therefore, that in the case of the *infra-hominid* hairs the medullas begin to appear (in the form of the *discontinuous* medulla) when the hair shafts have attained a diameter of about 15 microns; and that in the *hominid* hairs they do not begin to appear until the hair has reached a diameter about twice as great.

The fact that the human head-hairs do not show the *discontinuous* or the *intermediate* types of medullas (those types which are so common among the *infra-hominid* mammals) and exhibit virtually no varietal differences away from the types shown in Fig. 4 is to be understood, it is believed, as being the medulla expression of the unity of the human species.

SUMMARY

The cuticular scales and medullas of the human head-hairs are related, as are the same elements in the hairs of

¹¹ Many of the *Primates* exhibit the *discontinuous* and *intermediate* types of the medulla.

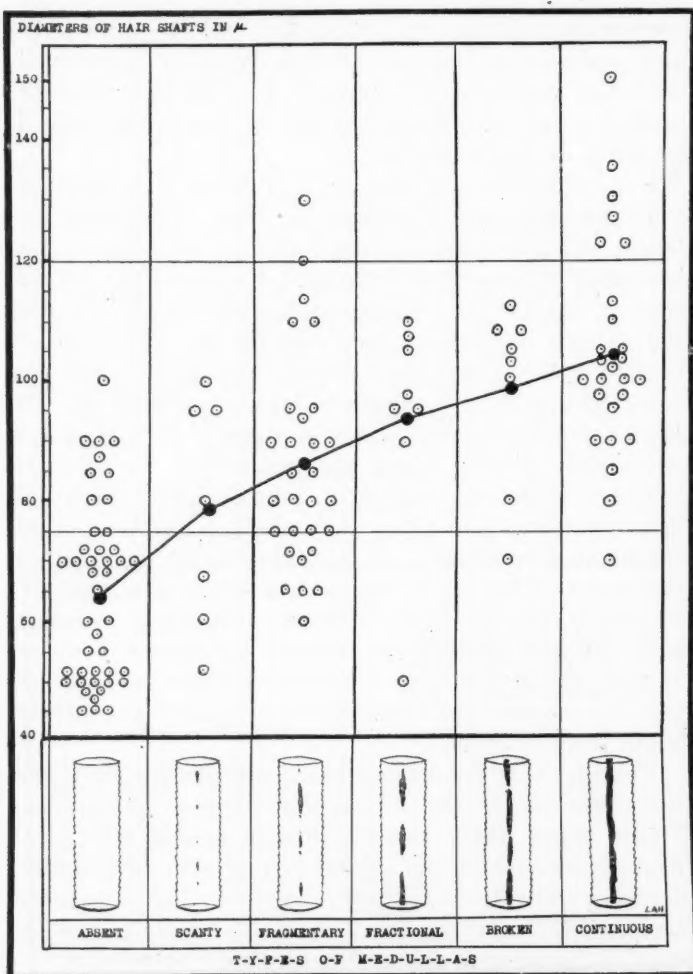


FIG. 4. Relationships between the medulla forms and the diameters of the hair-shafts as shown in 122 specimens of head-hair from individuals representing all the existing races of mankind.⁷ Clear circles represent the individual data. Along the abscissa are pictorially defined the terms descriptive of the conditions of the medulla. The determinations were made, in each case, midway between the base and the tip of the hair-shaft.

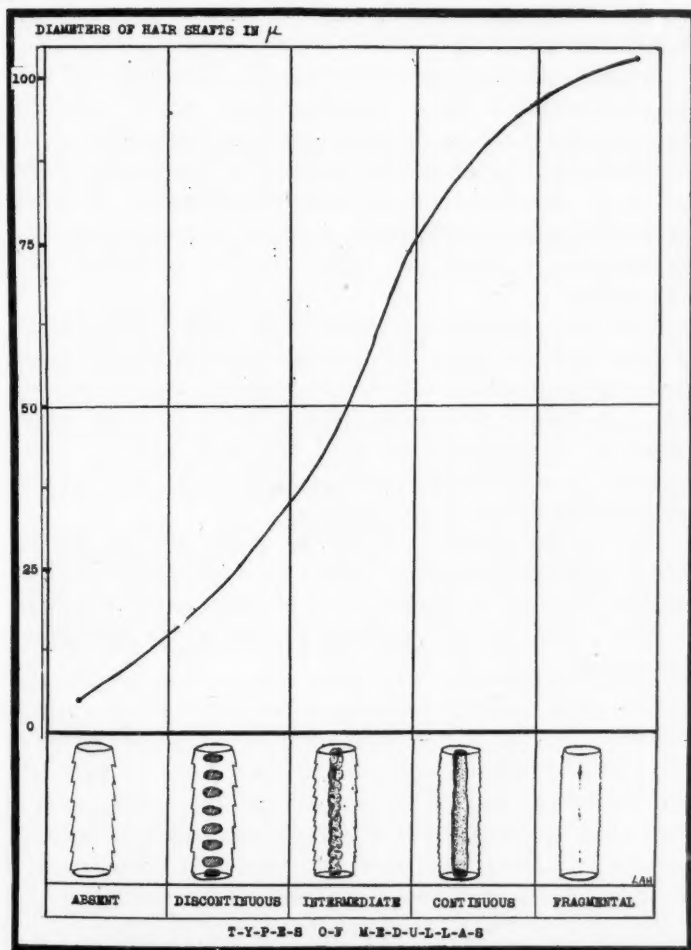


FIG. 5. Relationships between the medulla forms and the diameters of the hair-shafts as shown in 170 species of mammals below the *Hominidae*, and representing all the existing orders except the *Cetacea*. Along the abscissa are defined the terms descriptive of the conditions of the medullas. The determinations, in each case, were made midway between the base and the tips of the hair-shaft.

the *infra-hominid* mammals, to the diameters of the hair-shafts. They can not be considered, primarily, as characteristic of race.

Human hairs have not been found to show any but one type of scale, *i.e.*, the flattened, nor any but the continuous and the varieties of the fragmentary medullas.

Neither the scales nor the medullas of human head-hair show any of those characteristic modifications of form which have been interpreted as being specific, or group, differences among the hairs of the *infra-hominid* mammals.

It is believed not to be possible to identify individuals from samples of their hair, basing identification upon histological similarities in the structure of the scales and medullas, since these may differ in hairs from the same head, or in different parts of the same hair. "Accidental," or unusually striking similarities can not, of course, fall within this category.

The gross qualities of human head-hair, *en masse*, seem to be much more accurately characteristic of ethnological groups of mankind (or at least more definitely usable) than do the microscopic units of the individual hair-shafts.

THE MIGRATION OF ANIMALS¹

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The behavior of the very highest animals is chiefly determined by intelligence and reason. But the behavior of by far the largest number of animal kinds is mostly determined by instinct.

WITH the above quotation a well-known scientist begins his review of a recent book. The present writer begins his article with the quotation principally because he does not agree with it. To consign activities of organisms for which we have no scientific explanation to the realm of instinct, thereby removing them from the realm of the zoological to which animal activities logically belong, is both a mistake and an unscientific procedure. We know little or nothing regarding instincts; the term is often used to cover a multitude of ignorance, a wealth of known facts for which we have at present no scientific explanation. By consigning these activities to the category of instincts we save ourselves the embarrassment of admitting ignorance, but thereby remove from the field of zoological investigation many problems essentially zoological. An instinct defies scientific investigation; we can not explain it on the basis of known facts, and a problem solved by obscuring it under the blanket of instinct is thus effectually buried and is no nearer solved than before the internment, though it is safely out of the way—at least for a time! To assign a reaction to the category of instinct should be the last, final act of the zoologist, resorted to only after every line of scientific investigation has failed to throw light upon the subject, and even then it must be distinctly understood that problems so assigned are merely in a temporary dwelling. “In-

¹ Contributions from the Zoological Laboratory of the University of Illinois, No. 258.

stinct" solves nothing: it but adds one more problem to problems already difficult enough, though it often throws a veil of misplaced conviction of solution about a problem. The migration of animals too often is classed as instinctive. The phenomenon of migration has still not been explained in most cases, as among the birds, for example, though literally dozens of explanations have been brought forward. The present paper does not purport to offer much that is new, but is intended rather to bring before the reader for his consideration a line of thought which the writer believes is too little considered, yet a line which is open even now to scientific investigation as yet untouched, and which is, in the course of time, subject to proof or disproof.

Migration is ordinarily defined as "a *periodic* passing from one place to another." At once two types of migrations present themselves: (1) daily movements and (2) seasonal movements. The difference between them is this: daily movements are primarily feeding movements, or reactions to light, while the seasonal migrations are ordinarily breeding movements. While the writer wishes to concern himself primarily with the second of these types, it is perhaps worth while to briefly enumerate one or two examples of the first type, the daily migrations, to which we have a more or less satisfactory biological answer, and which are ordinarily not classed as instinctive.

These daily migrations must be admitted truly migrations, yet they are of essentially a different type from the seasonal movements—that is, their *cause* is different. There is less mystery about them because we can make some reasonably scientific explanation for them. These daily migrations are, as has been indicated, of two types: (1) those movements which are due to light reactions on the part of the organisms and (2) those which are feeding reactions. True, this latter type may, in many cases, trace back to the former in the last analysis, yet the *causing* factor is quite different, though the *ultimate*

factor may be the same. As an example of migrations of the first category, we may cite the movements of the entomostraca. It is known that many species move upward at night and downward during the daytime. This is evidently a migration and a light reaction, as has been proved. At the present time we can go little beyond saying that the movements are due to a negative phototropism on the part of the organism, and by this we mean that the organism is physiologically not attuned to light and therefore avoids it. One would hesitate long before assigning instinct as the causing factor for the movement of *Daphnia* and *Cyclops*. As an example of the second type, the feeding movements, the writer cites the case which has come under his personal investigation, that of the cisco (*Leucichthys artedi*), the small lake herring found throughout the northern Mississippi drainage area. Entomostraca form a very large percentage of the food of these fish—almost 100 per cent. during certain months—and it has been found that these fish likewise are up at night and down during the day, corresponding to the movement of their food. To this type of migration, then, we likewise have an answer.

We turn now to the seasonal migrations, which are admittedly associated in some way with the breeding reaction. Among the fishes we have many examples. The salmon migration is well known. The pickerel (*Esox lucius*), leaves the deep waters of the lake as the ice breaks up, and spawns in the very shallow water of the marsh overflow. Among the reptiles we have the sea turtles, ordinarily shunning land, coming to shore to lay the eggs, and then returning to the open sea again. Perhaps the best known seasonal migration is that of the birds, details of which need hardly be presented here. The facts of bird migration are well known and well established; the cause of the migrations is not so clear.

Concerning this phenomenon of migration among birds, what explanations are offered to cover the facts? There have been so many ideas advanced that only a few of the better known are offered:

(1) *Food*: That food is the underlying factor causing bird migration is still strongly held by many observers. Undoubtedly food is a factor in some cases, but not in many. The ducks and geese go south in the fall with the closing of the lakes, but why did they go north in the spring? All birds leave the south when food is abundant and most return south again while food is still abundant in the north. Were food the factor causing migration, once south the birds would never come north!

(2) *Temperature*: That temperature determines migration is also strongly held. It has been shown that the robin comes north more or less coincidentally with a certain temperature wave. Yet no one has explained *why*. The determining temperature in the case of the robin is said to be 35 degrees Fahrenheit, yet robins winter where the temperature is well over this point many times during their sojourn in the south: why do they suddenly come north with it? Again, the swallows go south while it is still very warm.

(3) *Wind*: It has been shown that migrations occur during winds of certain directions. I do not question the fact: I admit it, but I ask again, *why*? Surely during their stay in the south the migrants have been subjected to winds from every direction again and again; why did they not come north with that critical wind before?

(4) Humidity, pressure, etc., and a host of other factors have been advanced to explain migration, yet the *how* and the *why* is not clear. The same may be said of the idea most recently advanced, that birds migrate in the direction of the lengthening day. Nothing is here explained: one problem is substituted for another.

(5) *Breeding instinct*: Here we come to the "zoological buck-passing." Birds come north to breed and when they are done they go back south again. Simply perfect, but not, alas, perfectly simple! This would be, according to the quotation cited, the final answer. I offer that it is unsatisfactory.

(6) Physiological changes going on within the body, mainly in the sex organs. Here is the crux of the whole

matter, and the hub around which this paper turns. We shall deal with this at some length shortly.

The point that I would make is this: that, with the possible exception of the sixth, not one of these answers explains *why* birds migrate, and the sixth is not very clear about it. I believe that they fail to explain it because not one of them takes the bird *itself* into consideration; all are attempts to explain the movements as due to external factors only. And this is but natural perhaps, because we know a good deal about externals and very little indeed about internals! Yet I believe that the internal factors are of the utmost importance. Not that I would discard the external influences, but I would erect internal factors upon which the external conditions may operate. Not food nor temperature nor wind nor length of day explain migration *unless there is an internal mechanism upon which they can operate*. Then, and only then, may one or all of them operate, not as causative agents, but as secondary effecting or contributing factors. So much for the theories of migration. Let us now turn to a consideration of other matters which will lead us back eventually to the subject in hand.

Since migration concerns the distribution of animals, we may well ask the question: What determines the distribution of animals? While there are several answers to the query, the one with which we are concerned may be discussed very briefly under the title of "regulatory mechanisms." We are not concerned with physical barriers as limiting agents.

Those who have studied along the lines of physiological ecology are familiar with the fact that the animal body is a complex of regulatory mechanisms which regulate the body activities of the animal and, through these, may regulate the distribution of the species. Such regulatory mechanisms as those associated with respiration, hydrogen-ion concentration, enzyme, water and temperature regulation are known. Only one of these will be given as an example to illustrate my point: the respira-

tory regulation. Let us take the case of the mountain sheep which lives in the high altitudes and which has no physical barrier to keep it from coming down into the plains. But it does not come down. When the sheep descends to a certain level it turns around and goes up again. Why? As the animal descends the mountain, the air becomes denser and, to borrow an apt expression from Dr. Shelford, "its carbureter is regulated to light, high air." As it comes down, the sheep gets too much oxygen and the respiratory rate is decreased, as animals have a capacity to use only a certain amount of oxygen. The animal simply can not live under the new conditions, and must return to conditions suitable to it as it can not adjust to the new conditions. In our own case the converse is equally true: when we go up into high altitudes we can not attune to the light oxygen pressure. At high altitudes the solids in the blood increase, due to a transfer of fluids into lymph. When the blood contains too much lactic acid this acid affects the respiratory center and causes difficulties. Were man not a reasoning animal he would be barred from high altitudes as the sheep is from the low.

These various regulatory mechanisms are all bound up together, with the result that every animal has the capacity to regulate its conditions, but this regulation is limited to the usual fluctuations of its natural and normal environment. When fluctuations pass beyond that point the animal can not adjust to them. Thus an animal regulates through behavior by the following steps: (1) Certain processes are going on within the animal; (2) external changes affect the rate of these processes and upset them; (3) the result is movement of the animal in an attempt to adjust to the changes; (4) these movements bring the animal into various conditions, one of which may relieve the disturbance, in which case the disturbing factor being removed, movement would cease, as the equilibrium between processes and environment is established. By these steps we see that the environment of an animal may be regulated by behavior, *e.g.*, movement.

These statements all assume changes in *external* conditions, which change is followed by movement of the animal due to the upset of the equilibrium that must exist between the internal processes and the external conditions. The animal is comfortable only when it is in a state of stable physiological equilibrium with its environment. External change upsets this condition. Now let us ask this question: *Suppose* the change should be *internal* instead of external: would not the same results be manifested? Such an animal is no longer in a state of congenial physiological equilibrium with its environment. The conditions are the same in both cases: the carbureter is out of adjustment to the conditions! Would not movement result as in the former case? I believe it is logical to expect that it would. Therefore, if we could establish the existence of periodic internal changes going on coincident with the periodic movements of the animal, we might demonstrate the movement as being caused by such changes. Such, at least, would be a possibility. Since migration is an example of this periodic movement, then we might explain migration as being caused by these internal changes. Are there in reality any changes going on at the time of migration? Can we establish internal changes sufficiently marked to throw the organism out of equilibrium with its environment? I believe we can, and I think that we can go farther: I think we can show what is *causing* the internal change. Since these migrations with which we are dealing are admittedly breeding or reproductive in nature, let us turn to a consideration of the reproductive cycle.

To the student of modern ecology the term "physiological life cycle" is well known. By it is meant the sum of all the physiological states an organism passes through from the egg or young to the adult. This in itself recognizes the fact that an animal is a complex of physiological states, and that these states vary during the life process of the animal. Among the various points which might be emphasized in connection with physiological

life cycles one interests us particularly, namely, that the physiological changes are *rhythmic* in nature—that there is a fixed sequence of physiological states beginning with the breeding adult, passing through the egg, young and old larva, pupa and adult stages (as in the case of the Tiger beetles worked out by Dr. V. E. Shelford) and finally the sexually mature adult. Dr. Shelford has shown that this sexually mature adult returns to a physiological state essentially like that of the young and that they are physiologically equal. The female selects the place for oviposition, and at this time she is in a state of physiological equilibrium with the environment selected. The young hatches in this environment and is likewise in physiological equilibrium with that environment; therefore the female, when laying her eggs, has become physiologically a larva. Dr. Shelford has shown that moist sand is preferred for the laying of the eggs. If this sand becomes too wet the larva will burrow and wander until a new place is found under conditions that are similar to those chosen by the female when laying the eggs. These congenial conditions being found, wandering ceases. Hence the female and the larvae are physiologically alike, and there is no instinct involved in the selection of the breeding grounds; it is a matter of physiological balance. This point is emphasized as I hope to show that this idea can be applied to certain phases of bird migration. For example: It has been demonstrated that the young of some species of birds (robin) show upon leaving the nest a tendency to move northward. This is often held up as a strong evidence to prove that migration is an *inherited instinct*. However, if we admit that the young at the time of immaturity are in the same physiological state as the female at the time of laying the egg, then, if the female was at that time under physiological urge (which we will discuss in a moment) that accompanied a northward migration, is it surprising to find the young temporarily responding to a like physiological state? I think not. Thus this northward migration becomes a response

to a physiological state, not a reaction to inherited instinct.

It is well at this point to investigate for a moment what is going on, physiologically, in the reproductive cycle of the higher vertebrates. As the female of the human species approaches the period of sexual maturity, we find marked physical changes occurring throughout the body. These changes are internal as well as external, mental as well as physical. The internal metabolism is markedly increased, fat is deposited, bone deposition increases, the composition of the blood changes in regard to erythrocyte and leucocyte content and, when the period of menstruation occurs (the proöstrum) we find the female a totally different organism from a physiological point of view. The female, at the time of ovulation, has reached the climax of a series of physiological states through which she has been passing. If fertilization occurs during the oestral period, then a new series of physiological states is initiated, through which the female passes, slowly returning to normal only after the birth of the young. If fertilization does not take place, the return to normalcy is much more rapid. In either case, however, it is a *periodic* and *rhythmic* cycle, a fixed sequence of physiological states.

In the case of males of animals that are not permanently in a state of sexual maturity we find a corresponding series of changes, reaching a climax at the time of maturity of the spermatozoa, and declining again to normal after the breeding season. In the case of the male, as the climax state is approached, one finds the development of the secondary sexual characters, and the sexually functional male is essentially a different animal physically and physiologically from the immature or non-breeding male. This change is expressed not only in the physical make-up of the animal but also in its activity. The sexually mature female likewise expresses her change in physiological state by a change in behavior, as in the case of the salmon, the dog, the birds. Thus we

can see that the sexually mature animals are different from the non-functional animals not only in physical appearance in many cases, but also in behavior, activity, mental condition—all of which is simply saying that they are in a different physiological state.

Do we know what brings about these changes? We believe we do. Almost endless experiments have shown that these so-called secondary sexual characters and the changes that result during the season of "heat" or "rut" or "desire" are due to the activity of the sex glands. The clasping reaction of the male frog, which results in amplexus, occurs only at the height of the breeding activity, and Steinach (1910) shows that if the testes are removed the clasp reflex is abolished. The effects of castration of both sexes are too well known to demand listing. Thus the sex glands become responsible not only for the development of secondary sex characters, but also for the *behavior* of the animal during the period of activity of the gonads. For the purpose of our discussion it might be well to class behavior under gonad influence as a secondary sex character, which it surely is. Is not migration, then, being a behavior expression of physiological change accompanying gonad activity, from one point of view at least a secondary sex character? Is it not closely associated with the development of secondary sex characters in migratory forms—as the morphological changes in the salmon and the plumage and song alterations among the birds? Since secondary sexual characters, which are ordinarily considered as being *physical* changes in the animal, are admittedly stimulated or repressed by gonad activity or inactivity, is it not conceivable that migration, a *behavior* change at the same time, is likewise an expression of gonad activity?

This brings us inevitably to the question of how the gonads bring about the changes so evidently traced to them. It is a well-known fact that the gonads produce both an *external* and an *internal* secretion. The external secretion is the *gamete*, the internal secretion a *hormone*.

Many proofs of this hormone secretion as the causative factor in the production of secondary sex characters exist. Castration, if carried out before puberty, prevents entirely the development of these characters. Periodic menstruation is indicative of a normal ovary; if the ovary be removed, the phenomenon no longer occurs, but will begin again if ovarian transplantation occurs.

In the gonad itself two types of cells are responsible for the two types of secretions, and it is the *interstitial* cells which are the hormone source. These cells lie entirely outside of the tubes that produce the external secretion and are quite definitely separated from them. It is possible in the male to tie off the tube containing the sex elements, thus causing them to disappear entirely. What is the result? The interstitial cells remain, and the point is this: that in such a case the sex instincts remain as strong as ever and the secondary sex characters develop normally. If the testes of a buck are exposed to X-rays the generative cells are killed, but not the interstitial cells. The antlers of the buck undergo no change whatever, while if the buck were castrated—in which case the generative cells as well as the interstitial cells would be lacking—the antlers would be lost. Thus we see the effect of the hormone secretion of the interstitial glands. The work of Steinach, Brown-Sequard, Voronoff and others points clearly to this. That the blood stream is the carrier of substances indispensable to reproduction was shown by Von der Heide, who injected foetal blood serum into a pregnant woman and evoked labor pains. The source of this hormone in the female has been shown to be the corpus luteum. L. Loeb (1911) has shown that the corpus luteum prepares a hormone which sensitizes the uterine mucosa so that it reacts to the stimulation of the ovum, with the production of the maternal placenta. He has also shown that this sex hormone produces the changes in the breast as well as the fact that menstruation is due to an influence emanating from the ovary during ovulation and, reaching the uterus, causes a severe con-

gestion which produces menstruation. That similar changes, due to similar causes, are going on in other higher vertebrates can not be doubted, though in a vast majority of cases no demonstration has been attempted. We still know practically nothing of the physiological changes in birds, but a supposition that assumes a similarity of circumstances is not out of place since we know something of hormone behavior.

Let us look at some other vertebrates and see how things stand. We know that in the case of the dog each breed has its own breeding cycle and that individual females possess their own individual cycle to which they remain very constant, irregularities occurring most noticeably with advancing age. We know that there are profound changes going on internally in the female as the breeding period approaches. The proöstrum is evidenced externally by the swollen vulva and the discharge of bloody mucus. This discharge ceases with the beginning of the oestrus, or period of desire, which lasts from seven to ten days. During this time the female is a very different animal: ordinarily quiet, she now takes to roaming and is incessantly on the go. Dog breeders tell us she is looking for a mate, but is this activity not merely a response to hormone secretion? Have not the hormones produced during the processes going on internally thrown her out of physiological equilibrium with her environment for the time being? Remove her ovaries so that the corpus luteum can not form after ovulation, and she does not roam. Are these roamings not periodic? Then they come under the definition of migration: they are a type of migration. Take the case of the frog. In the spring the males precede the females to the pond, and we find that they are sexually mature first. Does not this in itself indicate a sex complex? The same is true of many species of fish. In the spring the pickerel migrate into the very shallow water of the marsh overflow. The male is mature first and may precede the female. In my work on the cisco I find the males preceding the females

in the breeding migration by several days, and that they are sexually mature first. In the case of birds the males of some species migrate ahead of the females—the red-winged blackbird and penguin are cases in point. Non-breeding birds often do not migrate nearly as far as do the breeders: the herring gulls that remain far south of the breeding grounds are non-breeders. Do these facts not indicate a sex complex in connection with migration? The singing of the male bird is characteristic of the spring migration and the period following. Why does he sing? Is he happy? Probably he is no happier than he will be a little later in the season when he is silent. His metabolic processes are speeded up by the activity of his reproductive hormones and the result finds expression in song as in other species it may find expression in color or plumage modifications or odd actions, as the dance of the prairie chicken and the drumming of the grouse. We know these phenomena as secondary sexual characters and it would seem that they are due to hormone secretion. Yet, among our song birds at least, they occur only in connection with the migration. Does this mean nothing? It is far too general and far too common to be of no significance.

Another point. The big waves of bird migration occur almost at the exact date year after year, irrespective of the weather *to a very large extent*. If external factors alone were responsible for migration the birds would arrive almost any time. But an organism among the higher forms has a definite cycle through which it passes—a very definite series of physiological states which are passed through in sequence and which are not materially hurried or retarded by slight changes in external conditions. Therefore it is not surprising to find the migration waves occurring year after year with surprising regularity, and to find that year after year the same species are found in the same migration waves. Species having similar breeding cycles find themselves migrating at the same time, just as they find themselves developing bright colors or singing or dancing at the same time. To me

these are all expressions of one and the same internal cause: hormone secretion.

As we have thus far based our discussion on the idea of internal change due to a hormone cause, the question naturally arises: is this pure speculation? Is there any ground at all to support such an idea? I believe there is, and would call attention to the interesting case among cattle, known as the "freemartin." The freemartin is a sterile individual cotwin to a normal bull calf. The work of Lillie has shown that this sterile individual is a sexually undeveloped *female* in spite of the fact that it shows unmistakable secondary sexual characteristics of the *male*. Embryologically the freemartin and its normal male twin are dizygotic, but monorchordial. There is established between the twins a direct blood flow, so that the arteries of the twins are in direct connection. Thus the blood of one foetus circulates freely in the body of its twin. Now, the male is throwing off hormones into the blood and these, carried into the body of its female twin, repress the normal development of her reproductive system and at the same time stimulate the development of certain secondary male characters. Thus we find a profound internal change due to a hormone cause: not only a nullification of sex, but a development of secondary characters of the *opposite* sex! These facts show further either that (1) the male hormone is stronger than that of the female or (2) that it is developed earlier and so gets a head start in its activities. Either of these ideas might well explain why in some migratory species of birds one sex (the male) always precedes the other in the northward movement. Another case: The obstetrician knows of cases where newly born girl babies menstruate shortly after birth. The explanation lies in the fact that the child has absorbed from the mother certain hormones which, had the mother not been pregnant, would have caused her to menstruate. A contribution by Poehl, Zoeth and Pregel may prove to be of great importance. These men have shown that "spermin," the hormone produced by the testes, lessens fatigue and causes an increase in the

amount of muscular work that an individual may accomplish. This is indeed very significant when one considers the astonishing distances covered during migrations and the tremendous expenditure of physical exertion involved.

If these things are true, then what are we to say about the non-migratory species? Simply this: that their tolerance is greater than in the case of migratory species. Barring physical barriers, an organism is limited primarily by the *range* of its regulatory mechanisms, as we have already pointed out, and by the *degree* of its adaptability. Non-migratory species are such because the degree of physiological change due to the activities of the gonads is insufficient to throw them out of harmony with the environment: their range of tolerance is greater. It is a noteworthy fact among our birds that do not migrate that there is relatively little development of marked secondary sexual characters, as in the English sparrow, the downy and hairy woodpeckers, the crow—while a vast majority of migrants show decided development of either plumage or voice. Furthermore, that migration is not a response to external conditions is hinted at by the fact that when a non-migratory species is transplanted from one continent to another, it remains a non-migrant, as in the case of the English sparrow and the starling.

Again, I believe that specific differences are more than a matter of color of a feather or number of primaries or length of toe. I believe that species are physiologically and perhaps cytologically different. With this idea in mind, I do not find it surprising, therefore, to find the striking differences between closely related species. Close gross structural relationship does not necessarily imply similarity in physiological states. Among the plover, for example, it is not surprising to find the far-reaching migration of the golden plover and the relatively limited migration of the killdeer. It is simply a matter of degree of change of physiological states, coupled with a varying range of tolerance. Other things

being equal, the greater the change the greater the migration.

There is yet another phase that, while not directly in line with a discussion of migration, is in line with a consideration of physiological state and change which we are discussing, a phase which I believe has for the most part been overlooked. It has already been pointed out that the breeding female is in an essentially different physiological state from the non-breeder. The most marked change is a change in her behavior as expressed in terms of nest-building and incubation, two closely related phenomena which are conspicuous in the non-breeder by their absence. Therefore, they form a part of the breeding cycle and an external change due to an internal hormone cause. These phenomena are ordinarily held up as examples of parental instinct, maternal affection, intelligence and what not. Let us examine them for a moment. In the petrel we have a bird that spends its entire life over the water, flying over the waves of the oceans for months on end. At the breeding season the birds come to land, build their nests and incubate, a most radical departure from their normal mode of life. The same is true of the albatross, the gulls, the terns. The breeding bird sitting on her eggs is, physiologically, a different bird. What is this difference? Expressed in ecological terms, she has become "thigmotactic." The approach of this thigmotaxis is first seen in the nest-building: the moulding of the nest to the body. Here is your petrel or gull or albatross or robin suddenly seeking the thing which all its life it has avoided—general contact with surfaces. The bird gouges out a depression in the sand or constructs a nest, moulding the contour to the curvature of the breast. The thigmotactic response reaches its culmination in the three or four weeks of patient incubation: how different from the normal behavior of the bird! This thigmotaxis wears off again in the course of time, particularly evident if the eggs do not hatch: the bird does not sit indefinitely. In the case

of the woodcock, so strong is this impulse that it is possible to walk up to an incubating bird and lift it from the nest by hand and eventually replace it. This is often paraded under the title of "protective coloration"—that the bird trusts to its resemblance to its environment for protection. While I believe in the existence of protective coloration, I do not believe that the woodcock has such unbounded faith in the theory as to permit itself to be handled. On the contrary, I believe that the thigmotactic response is simply too much for it to overcome—stronger even than fear. From this point of view, then, nest-building and incubation become thigmotactic phenomena accompanying the culmination of the physiological changes due to the reproductive cycle, and are, like migration, expressions of a hormone cause.

An animal in nature is in a state of stable equilibrium with its environment. Any change on the part of the environment must be met by a corresponding change on the part of the organism either by (1) an adaptive reaction to enable the organism to meet this change; or (2) by a retreat of the organism. "The disharmonic organism must attune itself or perish." Since, therefore, an environmental change produces a reaction on the part of the organism due to the upsetting of the equilibrium which must exist between that organism and its environment, it is reasonable, as we have shown, to suppose that a change on the part of the organism which throws it out of physiological equilibrium with its environment is capable of causing the organism to move into a new environment. Since an animal in the breeding season is physiologically a very different animal from the same organism in the non-breeding season, and since the change is due primarily to the activity of the gonads, it follows that the movement of the organism which causes it to seek a new environment (in which it becomes at least temporarily a balanced unit) is due directly to the activity of the gonads. Thus migration becomes an adaptive response to gonaactivity, and since this activity is a hor-

mone secretion, migration becomes an *effect* to a hormone *cause*.

This idea of migration as an external expression of an internal urge takes all idea of abstract instinct out of the problem. It does more than that: it gives us a concrete basis for explaining the changes that accompany the appearance of the breeding season and a basis that is subject eventually to proof or disproof by scientific procedure. Just how the hormone of the sex glands brings about these changes can not as yet be stated: our knowledge of hormone activity is as yet very inadequate. So we come here to a locked door. But there is a light under the door which shows that there is something on the other side, and it is confidently believed that the key to the door is not lost, merely not yet found. Perhaps there is a change in the hydrogen ion concentration of the body: there is a hint of this in the only published work done on hydrogen ion concentration of pregnancy, by Löb and Higuchi (1910), where the investigators found an ion concentration of the normal placenta of pH 7.65 and that of the foetal placenta pH 7.96. In closing, a word to those who hold that migration is due to wind or temperature or pressure or humidity or length of day: hormone activity changes the entire physical status of the organism and thereby may, perhaps, form a basis for the organism's reaction to wind or temperature or what not, by having upset the internal equilibrium and by increasing thereby the organism's susceptibility to external change.

DINOSAUR EXTINCTION

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THE riddle of dinosaur disappearance excites wonder. That stupendous group lived through all Mesozoic time, showed considerable plasticity, reached armor specializations paralleling those which seem to give the Testudinata an exceedingly long lease of life and finally increased its numbers in relatively modern environments. Yet the higher or more bird-like types, the sauropods, the carnivores and many armored forms all alike vanished almost instantaneously as geologic time goes. Such an obliteration seems strange in a world "which makes its own climates."

A searching analysis of the fine fossil vegetation of the English lower Greensand reveals a barely subtropic climate, though some dinosaurs were there present. Equable and varied habitats were always left over to the dinosaurs, as their range through the higher latitudes was in any degree restricted or cut off. Nothing clearly known of food habits or of early Tertiary climates explains that abrupt ending. "There was little about the dinosaurs prophetic of their fate." What then were some of the invisible influences that undid them? Were the greater enemies those within or those without the phylum?

Thirty years before the discovery of the Manchurian eggs, Forsyth-Major, assuming that reproduction was by means of eggs, averred that the sauropods especially were brought to extinction by raids of early mammals on the eggs. The view is also more or less correctly attributed to Cope. But the hard tough eggshells of many of the dinosaurs could not readily have been broken by most smaller animals, and the behavior of the varanid lizards shows that all really formidable egg-eaters unite

with great activity in the habit of swallowing eggs whole. The potent feeders on dinosaur eggs and young must be sought for amongst the dinosaurians themselves—and perchance, amongst the earliest varanids and boids, both of which reached immense size by Eocene time. Any enemies within the early Creodont lines are altogether hidden in the background.

Struthiomimus, the “ostrich mimic,” and *Ornitholestes*, the “bird robber,” have had the attention of paleobiologists. These were the weaker carnivores, the kind becoming toothless towards the close of dinosaur times. *Laelaps* and the other large carnivores have been freely pictured in combat with the sauropods or fighting amongst themselves, and the view is not unreal. I well remember Cope’s classroom remark that “*Laelaps* was one of the most aggressive and formidable animals that ever existed.” But the idea presented here is a somewhat different one of incessant egg robbery, of continual prowling throughout the egg season, and then the hunting down of the young.

A further item in the carnivore *menu*, serving when other food grew scarce, and also suggested from the habits of *Varanus* is easily understood. Just as I found with the skeleton of the great Pierre turtle *Archelon* a single tooth of a shark, identified by Cope as a broad-toothed *Lamna*, so I found a single weakly serrate, rather flat carnivore tooth (*Allosaurus*?) with the vertebrae of the giraffe-necked sauropod *Barosaurus*. In both instances scavengers are probably indicated.

The plant-eating dinosaurs were numerous. They had an immense range in space and time, and the point is suggested that their eggs, eaten during a season of some length, were one of the stimuli to increase of size in the carnivores; that these after a time became very destructive, and (somewhat overgrown) were in turn subject to the loss of eggs and young due to the depredations of animals less powerful than themselves. It was in the midst of such life that mammalian viviparation became, partly of outer necessity, a fixed mode of reproduction.

Neither size, number or nutritive value of reptile eggs now or in the past is in doubt. In the markets of Burmah, Varanus eggs are esteemed and sold at a higher price than hen's eggs. Free from all disagreeable taint, of finest flavor, the white does not, as in fowls' eggs, coagulate on boiling; and these same fine qualities I have found in eating the eggs of the wood tortoise. The flesh of reptiles may have a protective rankness or even a poisonous or injurious quality, as in some of the turtles, and the eggs yet be wholesome.

Tyrannosaurus, amongst all carnivorous dinosaurs, most suggests a growth and habit due to some increased abundance of prey. What more likely than that the immediate ancestors of this dinosaur got their first impulse toward gigantism on a diet of sauropod eggs, and that, aside from the varanids, the theropod dinosaurs were the great egg-eaters of all time? The idea does not preclude a final increase in size passing the limits of food supply and so tending toward extinction. Very great sizes in organs or individuals may pass the vantage point through inertia; and evidently the dinosaurians so suffered.

That the earlier varanids and boids also aided in the final destruction of the dinosaurs would be quite inferable, were the skeletal remains of all found associated in the fossil quarries, and that they are not so found may be due to accident or habitat. Just as the dinosaur record closes, the great Eocene varanid of crocodilian size from Wyoming described by Gilmore and also the boas (*Paleophus*, *Boavus*, *Dinyllisia* of the older Eocene) appear. Such giants had ancestors somewhere in late dinosaur times. Both varanids and boids retain great size throughout Tertiary time, and both seem to have passed the acme of their development but recently. The varanid *Miolania prisca* Owen, of the Queensland Pleistocene, was a startling reptilian thirty-three feet in length.

Falling far short of such proportions, the varanids of to-day are nevertheless formidable marauders. They are seen all over the Old World tropics from desert to

jungle, preying on the largest animals they can master. They climb trees, are expert swimmers, and, though hiding their own eggs in hollow trees, are everywhere great prowlers and egg-eaters. Their traits and habits afford a veritable foreground to the portrayal of carnivorous dinosaurian life—dissimilar, mainly, as indicated by pneumatic and other birdlike skeletal features, and a prevailing bipedality. *Varanus salvator*, the great monitor of Ceylon, or “kaboragoya” is the largest living lizard, having a length of eight feet. As Ditmars significantly relates:

This powerful brute is partial to the jungles. Few sportsmen have been through such a country without occasionally being startled by the rush of a monitor ahead, making as much noise as some hoofed animal as it tears its way through the undergrowth. The methods of attacking a small animal resemble more the actions of a warm-blooded animal than a reptile. Rushing for the ill-fated creature at a gait rapidly overtaking it, the lizard seizes the prey and shakes it in the same violent fashion as a terrier shakes a rat. If the animal's struggles become so violent that its escape is rendered possible, the reptile holds it to the ground under its strong claws—as long as those of a fair-sized leopard, while the jaws take a better hold. The animal is then swallowed whole.

A caged example had a great appetite for eggs, as Ditmars continues:

Like all monitors, this one is fond of eggs, taking eight to ten hen's eggs at a meal, swallowing them entire and with such rapidity that the eggs come in contact with each other in passing down the throat, producing a clicking sound that can be heard plainly by one standing nearby. Digestion is rapid. Within twenty-four hours the gastric juices have thoroughly disintegrated the shells which are broken by compression of the stomach. Lizards and snakes are also eaten by this monitor.

Turning again to possible dinosaur habits the view presented is that the tooth-set gape of *Tyrannosaurus* is not inconsistent with nurture on sauropod eggs. Limning in the picture, it is *unlikely* that the dinosaurs merely dug in their eggs (certainly not the more bird-like forms), and it is *likely* that some care was given to the eggs and the young. Certain frill lacerations in Ceratopsians are held by Lull as possibly due to conflicts among the bulls, and such contests in higher animals at least indicate copulatory interest and go with maternal

care. Probably, too, the dinosaurian group being such a varied one, the carnivores were the more active blooded kind, whence the sauropod females may be imagined guarding their eggs as does one of the Boas. While as the days passed and the hatch shifted along the belly or the coiled tail ever ready to strike, the alert *Tyrannosaurus* gathered up any scattered eggs. Or the eggs if left unprotected would be the more quickly raided. The young, too, must have been subject to raiding and "cutting out," as in mammals. Perhaps the carnivores at times became social, hunting eggs and other booty in droves. With such active and powerful beasts at the jungle-edge, life was varied and sanguinary, be it within scientific dignity to say so.

How the dinosaurs lived and produced their young becomes less obscure as the facts of distribution and association are assembled. Thus the frequency with which dinosaurians of varied type are found in marine beds leads to a suspicion that there was a certain degree of seasonal dependence on water habitats. Bayou protection in winter has already been suggested. How fossil occurrence might fail to disclose the essential or average habitat and life associations can be illustrated in this way. The great "leatherback" turtle often wanders out of the warmer waters of the Gulf Stream, becoming helpless within North Atlantic shelf areas of fluviatile deposition favorable to fossilization. In such instances the resulting fossils, if brought to light in some future age after the course of the ancient currents could no longer be fixed, would yield one-sided or even misleading environmental evidence. The lure that entices the leatherback so far from the equable limits must be the northern animal forage, accessible only by way of the warm currents. The true habitat of any vertebrate might well be defined as only the region within which the young are safely brought forth.

To those inferential ideas of reptilian traits and growth just outlined there is this one lesser but not unimportant limit to set. It is possible that the late Creta-

ceous and early Eocene record must be viewed virtually as it now stands. In that case the Varanid-Boid gigantism was not coeval with the last of the dinosauria, and merely followed early increase in mammalian prey; although the argument remains much the same. If the herbivore reptilians evolved or grew up on a changing pasturage, and that would only be following life's simplest way and mean, there comes into view the correspondent spur toward carnivore growth—more varied prey. Both stocks reacted to the nearest available food sources as they underwent the biotic cycle.

In the larger view, the experiments of zoologists show the profound effect of food-change on reproduction and growth; geneticists find progressive change a thing outside their observation, time thus being the first essential in the origin of new species; and the paleontologist sees plainly enough that phyletic development, once begun, inclines to rapidity, reaches a climax and may then slow down after a certain amount of senile variety. Extinction of the phylum pursues much the same course as its obverse, development; after the more general disappearance, a few isolated forms are usually left behind long ages after all the rest of their kind are gone. Taking an example from the invertebrate world, the rise and going out of the trilobite is thus portrayed by Walcott:

The trilobite slowly developed in pre-Cambrian time, reached its maximum in the Cambrian period, and continued on in full tide until well into Ordovician time when the sea bottoms became crowded with a large and varied fauna, and numerous enemies, some small and insidious, parasitic in nature, others large and powerful, appeared, together with various types which, while not physically antagonistic, were economically so in being better adapted to live in the same manner under the same conditions. It kept up the struggle, but already an ancient type, it had lost its juvenile race plasticity, and ability to modify itself to meet the new conditions. Never having penetrated into fresh or other non-marine waters, or into the deep sea, those havens of refuge where the relics of many ancient types may still be found, the trilobite, unable to cope with the new world in which it found itself, was consumed as food by its new enemies, both internal and external, and at the same time subjected to overwhelming competition, so that the individuals died off more rapidly than they could reproduce, and the race disappeared with the close of Paleozoic time. It persisted for many million years and left its remains more or less abundantly through about 75,000 feet of stratified rocks.

Briefly told, the dinosaurs lasted through as great a deposition of sedimentaries as the trilobites; though in duration they are far exceeded by the mammals which have so recently passed their zenith. Beyond any other race the dinosaur, after the great deployment, half way through his history, goes out with a mighty flash of variety; eight or more remarkable genera are already known from the American Lance (and Ojo Alamo) alone. But neither the food supply nor geologic change affords a direct explanation for such a sudden termination of all the greater divisions of the race. Nor does early mammal egg-eating do so. About all that can be said is that the greatest enemies of the dinosaurs seem to have been of their own kind, and that perchance early varanid egg-eating and both varanid and ophidian attacks on the young brought them nearer the end, if any survived into the Eocene.

So stands the riddle. Was there some more recondite factor which forced the dinosauria out of the world's vertebrate life? Especially Abel, following somewhat Huxley and Marsh, sees much to emphasize in the bird-like features indicating early arboricolous, or tree-dwelling habits. The types on the borderland between the birds and the more terrestrial dinosaurs are expressively described by Abel as the Avidinosauria; and no one disputes the direct affinity implied. Nor can the avian resemblances in the skeleton of the dinosaurs lack a deep physiological significance in either their origin or their later expression. Other opinion *per contra*, that is why the dinosaurs were as a group warmer blooded relatively to the climates of their day than lizards and crocodiles are now, though probably not so warm-blooded as the early birds. I say taken as a group, because I do not suppose that the widely different families all had the same blood temperature. It is recalled that Baur, a keen anatomist, even argued that the Dinosauria were too varied to constitute a natural group. Any other temperature conception would amount to virtual denial of the potency of the geologic environment to produce warm-

bloodedness at all. Need any one be reminded that the great transition from very ancient life into mammals, birds and dinosaurs was simultaneous, and coordinated with the changes that led to the flowering plants? Whatever the primal impulse, reaction to it was at its peak in the late Permian and early Triassic. It involved as well the origin of the pterodactyls.

In truth, warm-bloodedness can only be a response to persistent and progressive factors common to all terrestrial environments. And certainly the most potential of such factors within any fairly uniformitarian purview of climate and the general course of cosmic change would be variation in respiratory nitrogen, oxygen and carbon dioxide, as mainly controlled by the oxygen release in the photosynthetic processes of more and more dicotyledonous forests. As expressed by Vernadsky, quoted by Nichols:

We know of not a single reaction in the earth crust which would liberate free oxygen except its production by organisms containing chlorophyll in the synthesis of their organic substances. At the same time we know of thousands of chemical reactions in the earth crust [and soil cover] which consume oxygen. If there were no chlorophyll bearing organisms, free oxygen in the atmosphere would long ago have ceased to exist.

Variable amounts of atmospheric carbon dioxide and some definite variation in the rate at which oxygen has been thrown off by successive floras are, then, a certainty. It can not be believed that the early Triassic forests of ferns, equisetes, seed ferns, cycads, cycadeoids, varied conifers, cordaites, ginkgos and pre-dicots and monocots set oxygen free at the same rate as the later Mesozoic forests. Moreover, it is likely that the withdrawal of carbon dioxide in the Pennsylvanian limestone-making and of carbon in the laying down of the coal were early causes of Permian glaciation; while another very great disturbance of the atmospheric equilibrium is indicated by the thick Cretaceous limestones. Generally speaking, the impression gained is that carbon dioxide, the breathing stimulant, mainly supplied from inorganic sources, grew less toward Tertiary time, and that although the areas of

ozone-laden air lessened as the greater conifer forests receded, respiratory oxygen tended to increase. And herein must have lain the elemental need and possibility of adjustment in the warm-blooded vertebrate life of the upper Mesozoic.

Nevertheless it was there, after having at first so sharply responded to the influences that brought about feathered and haired life, that the dinosaur lagged. The verge of progress was reached but never passed. It was left for other races to acquire flight, and at last even the science of mathematics! The organs of respiration were not very different from those of the birds in which the respiratory function reached intensity; the early reptilian stage was passed; the mammals were acquiring the smallest and most numerous of blood disks, so that in them the effective surface of organic interchange reached a maximum. The necessity for progressive physiologic change became tense as Cretaceous time waned; but the response, so far as inherently possible (or not inhibited by aplasticity), first came too slowly, and then overleaped the bounds. To a world that ever went forward, the final dinosaurian reflex manifested itself in absurd or fantastic armor patterns, little else than experiments in resistance to change.

At all points the dinosaurs that had trampled the earth till the grasses grew, the most superb of all vertebrates, the creatures that fix the imagination above all others, are seen to fail. The growth forces and the responses to environment were no longer in adjustment. Eggs were few, their loss from attack devastating, life slow. The young were the prey of their own kind, and the race had lived long enough for reptiles lower in life's scale to threaten. If new enemies were needed they were at the jungle-edge. Geologic change that once would have meant mere fluctuation in habitat affected the declining numbers disastrously, and what such change and the reptiles soon to rule in the forests of the Eocene may have failed to accomplish, senility did. That long dinosaurian day was done. Its sun was sinking beneath the horizon forever.

SHORTER ARTICLES AND DISCUSSION

SIZE OF COB IN MAIZE AS AFFECTED BY THE NUMBER OF FERTILIZED OVULES

SOME measure of yield often is desired in progenies of maize having a number of hand pollinated ears. Since hand pollinated ears frequently are fertilized imperfectly the actual weight of seed produced by them is not a fair measure of their yield.

For a number of years past we have made use of cob length and number of rows as the best expression of yielding capacity within or between closely related strains but recently evidence has been found in some progenies that the length of the cob increases in proportion to the number of fertilized ovules to an extent which if found to be general would vitiate yield comparisons based on the length of the ear.

This evidence appeared in data accumulated to study the factors influencing variability in the amount of cross-ingover in a hybrid between Chinese waxy and an Algerian pop corn. During the progress of this investigation we had occasion to measure the relative effects of single and double applications of pollen on a number of ear characters.

Quite unexpectedly these measurements showed that in addition to an increased number of seeds the ears resulting from two applications of pollen were longer and had more rows than those resulting from a single pollination. The biometrical constants for this population are shown in the following table.

From this table it is evident that ears having two pollinations produce more seeds than those having but a

| Character of Pollination | Cob length (cm.) | Number rows | Base of ear without seeds (cm.) | Tip of ear without seed (cm.) | Number of seeds | Date of ¹ pollination |
|--------------------------|------------------|-------------|---------------------------------|-------------------------------|-----------------|----------------------------------|
| Two pollinations | 18.44 ± .56 | 18.78 ± .38 | .167 ± .19 | 1.00 ± .21 | 586 ± 30.0 | 13.94 ± .62 |
| One pollination | 15.90 ± .24 | 17.44 ± .16 | .766 ± .08 | 1.22 ± .09 | 417 ± 13 | 18.45 ± .27 |
| Difference | 2.54 ± .61 | 1.34 ± .41 | .599 ± .20 | .22 ± .23 | 169 ± 32.0 | 4.51 ± .67 |

single application of pollen. Apparently this increase in number of seeds is accomplished by an increase in cob length, a reduction in naked base and an increase in number of rows, but curiously enough there is no clear reduction in the naked tip which for these ears appears to be a constant.

That the observed differences in length of cob and in number of rows can be attributed definitely to the number of pollinations is not so clear since there obviously is a significant difference in the average date on which double and single pollinations were made. This difference is entirely accidental, the second application of pollen being made according to the general appearance of the silks, but the observed relationship of single and double pollinations to cob length and row number may be simply a secondary one due to a possible correlation of earliness with these characters. To determine this point the correlations between these several characters may be examined.

COEFFICIENTS OF CORRELATION

| | No. of pollinations | Cob length | No. of rows | Date of pollination |
|--|---------------------|------------|-------------|---------------------|
| No. of pollinations ² | | .403 | .312 | -.637 |
| Cob length | .403 | | -.126 | -.239 |
| Number rows | .312 | -.126 | | -.010 |
| Date of pollination | -.637 | -.239 | -.010 | |

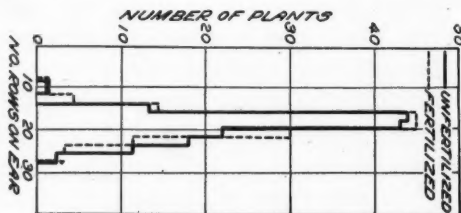
The table shows a significant negative correlation between date of pollination and cob length, indicating that in this progeny early plants have the longer ears. If the partial correlation is calculated for number of polli-

¹ Number of days taken from August 1.

² Biserial coefficients calculated for this character.

nations and cob length for constant date of pollination it is found that the coefficient is reduced from .403 to $.335 \pm .062$, a coefficient still too large to be ascribed to chance. The partial correlation between number of rows and number of pollinations for constant date of pollination is found to be $.395 \pm .059$, an increase from .312. Apparently the increase in ear size coincident with more than one application of pollen can not be considered as the indirect result of the correlation of ear size with earliness and the explanation must be sought elsewhere.

It seems not unlikely that in making second pollinations there is an unconscious selection toward large ears, since such ears would be likely to produce a larger number of silks following the initial pollination than would small ears and hence appear in need of additional pollinations. While this explanation of the observed differences would seem entirely reasonable, especially in view of the increase in row number, it was thought best to obtain further data before definitely rejecting the possibility of fertilization having a stimulating effect on the length of the ear.



Frequency distributions for number of rows on fertilized and unfertilized ears.

Since the ear of corn at the time of sexual maturity is very small as compared with its mature size, there is a possibility that elongation might be stimulated by fertilization in proportion to the number of ovules fertilized.

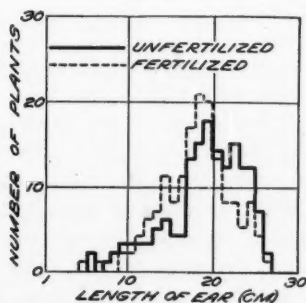
If this were true the maximum difference should be found when ears completely fertilized are compared with

unfertilized ones. To test this point a number of ears on plants chosen at random were protected throughout the season by means of paper bags, thus preventing pollination, and an equal number of plants were permitted to function normally. The strain chosen for this experiment was a variety of dent corn inbred for four generations. The results for cob length and number of rows are shown in the following table and the frequency distributions for these characters are shown graphically in Figs. 1 and 2.

| Character of pollination | Cob length (cm.) | Number of rows |
|--------------------------|--------------------|-------------------|
| Not pollinated | 18.705 \pm .2439 | 18.258 \pm .165 |
| Pollinated | 17.773 \pm .2142 | 17.747 \pm .113 |
| Difference | .932 \pm .325 | .511 \pm .196 |

It is apparent that these differences are in the opposite direction from those obtained with single and double pollinations. They offer no support to the hypothesis that the length of the cob increases with the perfection of pollination, but on the contrary they indicate that the growth period of the cob is extended to a slight degree in the absence of fertilization.

The difference in ear size observed with single and double pollinations, therefore, must be due to some unmeasured factor which influenced the choice of ears given two applications of pollen in such a manner that large



Frequency distributions for length of fertilized and unfertilized ears.

ears received on the average more pollinations than small ones.

While the increased length of cob on unfertilized ears is not significant in populations of the size used larger populations might establish the significance of this increase in length though this increase almost certainly would be less than one cm for cob length and but slightly over one half row for the number of rows. Such difference would be negligible from the standpoint of estimating yields in most progenies where only a small percentage of the plants are hand pollinated.

J. H. KEMPTON

BUREAU OF PLANT INDUSTRY

CHROMOSOMAL CHIMERAS IN THE TOMATO

IN a study of cross-sections of root tips from tomato plants grown from cuttings two plants were found in which certain roots were tetraploid either wholly or in part, while others were entirely diploid (24 chromosomes). At first it was thought possible that fusion of cells during the healing process of cuttings might have some causal connection with the production of the tetraploid cells. A similar explanation was advanced by Wink-



FIG. 1. Diploid chromosome group

ler (1916) for tomatoes which produced tetraploid adventitious buds following grafting with nightshade. While this possibility has not been entirely excluded for our material it is rendered improbable by the finding of a seed plant with a similar mixture of diploid and tetraploid cells in its roots. This plant was remarkable for the "wiry" or extreme "shoestring" character of its leaves which greatly resemble the leaf condition in an extreme case of mosaic. Probably both of the other plants with tetraploid areas were slightly infected with mosaic. It may



FIG. 2. Tetraploid chromosome group

be possible that local changes due to this disease might affect mitotic processes. The tendency to the production of cells with double, quadruple, etc., numbers of chromosomes in somatic tissues has been considered as an abnormal process related to degeneration as in the digestive epithelium of the mosquito (Holt, 1917) or as a response to certain specific external stimuli. Whether or not the latter can be proven to be the case in the tomato remains to be seen. Certainly the tetraploid areas in tomato roots do not represent degenerative changes. Némec (1903) first reported the production of tetraploid areas in roots by exposing them to narcotics. This work was repeated and extended by Sakamura (1920) who finds that the gall-producing secretions of *Heterodera* produce the same effect. Blakeslee and Belling (1924) found tetraploid shoots on diploid *Datura* plants after treatment with cold. It is improbable that cold is a causal factor in the production of the tomato chimeras since the roots alone appear to be affected at least in any degree. It should be noted that Winkler suggested that tetraploid cells already present might form adventitious buds following wounding. He thinks that this is not the usual cause because he found tetraploid cells very rarely in the shoots of the ungrafted plants which were examined. Thus far the affected plants have shown no tendency to produce gigantic shoots of the type of Winkler's tetraploid tomato. An attempt to obtain plants from root cuttings was a failure.

One of the main points of interest in the frequent occurrence of tetraploid cells in tomato tissues lies in the fact that triploid plants occasionally occur (J. W. Lesley and M. C. Mann, 1925). It is not yet proven that diploid gametes are produced, but if tetraploid cells exist in the shoot of otherwise normal diploid tomatoes as Winkler's evidence indicates, it is evident that such a gamete, if viable, uniting with a haploid one would give rise to a

triploid plant. Winkler's tetraploid plant was self-sterile and he does not report attempts to cross it with diploid.

The tomato plants from cuttings were normal diploid in appearance and except for the slight infection with mosaic they were not diseased. Interestingly enough the plants were diploid descendants of a triploid plant which makes the presence in them of tetraploid cells seem rather significant. It would be exceedingly difficult to prove that no tetraploid cells occurred in a plant and for that reason a good deal of preliminary work upon untreated plants would be necessary before one could attempt to attack the problem of causation of the chimerical condition discussed above.¹

In Winkler's material tetraploid cells were rare, but slight differences from the normal chromosome number were comparatively frequent. The reverse appears to be true of the roots of our chimerical plants.

In the chimerical tomato plants studied the entire root or only a few epidermal cells may be tetraploid. No two roots are exactly alike. In one a sector of tetraploid cells extended from

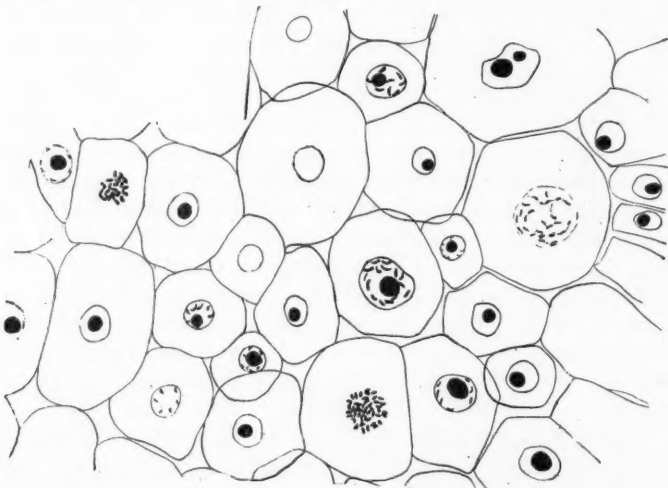


FIG. 3. Tetraploid and diploid regions in the same root

¹ In a root of an F_1 between *Crepis biennis* ($N=20$) and *C. foetida* ($N=5$) a few neighboring cells were found having about twice 25 chromosomes, whereas most of the cells contained the expected 25.

dermatogen to plerome and could be recognized in 77 sections of 8μ thick or for 616μ . Since the short first roots were studied the great extent of the tetraploid areas indicate that the chromosomal mutation occurred in the tissue of the shoot. The tetraploid cells are generally larger than the diploid ones, but it will be seen from the cross-section below (Fig. 3) that nuclei which by their size and by the size of the nucleolus which they contain indicate that they have the diploid chromosome number may appear in cells which look quite as large in cross-section as the one containing 48 chromosomes. The approximate areas of the cross-sections of the cells containing metaphase plates were obtained. The area of the diploid cell is 7.04 sq. mm in the original drawing, whereas the tetraploid cell is 13.86 sq. mm , or approximately twice the area at the equator of the spindle. The fact that the



FIG. 4

roots in the chimeras were not distorted shows that the tetraploid and diploid cells must have multiplied at **very** nearly the same rate. There is no indication that anything like a reduction division occurs in these roots, and Figs. 1 and 2 show that the chromosomes of the tetraploid are not abnormally shortened as was described for the tetraploid cells of plant roots found following treatment with narcotics, as reported by Némec (1903) and Sakamura (1920), nor do constrictions appear in them.

In the tomato difficulties in chromosome counting often arise from the fact that in root tip material fixed in chrom-acetic-urea the nucleolus gives rise to fragments not very different in size from the very short chromosomes. They are, however, usually slightly out of the plane of the plate and often do not appear at all, *viz.*, in the very late prophase just before the metaphase. The sort of thing which must be taken into account in counting chromosomes of this type is illustrated in Figs. 4 A and B and 5. The chromosomes are outlined, the nucleolar fragments solid black.

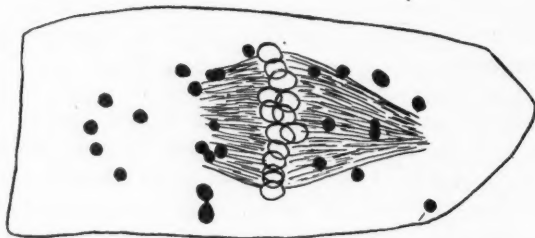


FIG. 5

It is evident that it is advisable that chromosome counts made from a few root tip cells in mitosis be checked by comparison with those of pollen mother cells at least in certain plants.

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